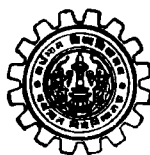


**STUDIES IN MONOCARPIC SENESENCE
OF PLANTS**

**THESIS SUBMITTED FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY IN SCIENCE (BOTANY)
OF THE
UNIVERSITY OF BURDWAN**

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JANUARY, 1991**

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Certified that the research work incorporated in the thesis entitled " STUDIES IN MONOCARPIC SENESCENCE OF PLANTS " which is being submitted by Mr Ruhul Islam Khan, M Sc for the degree of Ph D of this University, is an original piece of work done by him in this Department under my guidance and that the results of the present investigation or a part thereof have not been published or submitted for any degree elsewhere by any other person.

It is further certified that during the tenure of his research Mr Khan followed the rules and regulations as laid down by the University of Burdwan for the award of such degree.

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★ Chapter–1 ★

Review of literature on monocarpic senescence

1.1. Introduction :

Senescence may simply be defined as those deteriorative changes which lead, sooner or later, to the death of an organism or some part of it (377). Not only does senescence occur in almost all types of living organisms, it shows itself in different forms, even within the plant kingdom. In higher plants, single cell, group of cells or whole organs may be destined for senescence at what appears to be programmed times in relation to development of the plant as a whole. Unlike other developmental processes of the plant, senescence is the terminal phase of development.

There are two terms 'ageing' and 'senescence' which are widely used in reference to changes which impair the structural organization or functioning of living organisms. Whereas, senescence represents endogenously controlled active degenerative processes leading to death, ageing encompasses a wide array of passive or nonregulated degenerative processes influenced primarily by exogenous factors (207,287). This passive degeneration, termed ageing, is a consequence of lesions due to 'wear and tear' that accumulates over time and does not in itself necessarily cause death but may decrease resistance to stress or increase vulnerability to death (245, 287). Seeds in storage gradually lose their

viability and represent best examples of ageing (287). Thus, even if their developmental senescence programme is halted by preventing germination, seeds do not retain viability indefinitely. This degeneration may be due to gradual, time-dependent accumulation of lesions in DNA, the protein synthesising apparatus, membranes and probably other components of the cell (305, 426). There is reason to believe that these lesions are induced directly or indirectly by free radicals, reactive ions, and ionizing radiation, factors which occur naturally in our environment (330). However, our present knowledge is not good enough to define these processes more precisely or to draw a sharp distinction between them.

According to Osborne and Cheah (308), three important characteristics of senescence syndromes are : (1) progressive wear and tear with ageing and loss of ability to repair DNA breaks or lesions, (2) loss of membrane integrity and compartmentation, and (3) loss of homeostatic ability.

1.2. Types of senescence :

Cells are the basic unit of an organ or organism and it may be possible that all types of senescence are more or less alike (206) and basically similar at least at the cellular level (287), but the triggering actions may be different because death of a particular organ or a cell takes place at different stages of development. Leopold (206), on the basis

of morphological characters, has recognized four patterns of senescence : overall senescence (e.g., monocarpic plants), senescence of total aerial parts (e.g., perennial bulbous plants), progressive senescence of leaves from base to apex (e.g., bristle cone pine) and deciduous leaf senescence (e.g., winter shedding trees). Senescence occurs at different levels, from individual cells to tissues to organs to whole plants (206, 297). On the basis of this, Nooden (287) has recognized four patterns of senescence : cellular, tissue, organ and organism.

A somewhat different categorization of senescence behaviour pertains to flowering and fruition habit. Here we encounter monocarpic and polycarpic senescence. In the former, senescence and death ensue after the plant has flowered and borne fruits for a single time, this may not necessarily be annuals. In the latter category, the polycarpic-type senescence occurs only after many cycles of flowering and fruiting (451). While senescence-related changes in different tissues or organs of plants do show diversity, there are underlying similarities, especially at the ultrastructural level, suggesting that the processes of senescence are analogous (287).

Senescence of plant organs is a very common phenomenon in nature and has a great positive value from the ecological point of view. Organ senescence pertains to leaves (403), roots (147), flowers (243), fruits (391) and seeds (305).

The pattern of leaf senescence is varying in nature and different parts of a single leaf senesce at different rates (382, 446). The leaves of graminaceous plants senesce progressively from apex to base. The tissue around the vascular bundle seems to senesce later (50, 323), also the sieve tube remains functional until very late (240), possibly for nutritional purpose. In rice cultivars, two types of leaf senescence behaviour are reported, namely, sequential and non-sequential (257, 258, 259).

Monocarpic plants are mostly ^eharbaceous and undergo single cycle of reproduction, whereas, polycarpic plants are mostly perennial and undergo many reproductive cycles without intervention of death (153). According to Nooden and Leopold (291) monocarpic senescence is a carefully orchestrated retreat, rather than a plunge into chaos. Monocarpic senescence is the most remarkable post-reproductive development of the whole plant and exemplified by annual, biennial and even perennial plants. Some perennial plants, such as Agave americana (440), Corypha palm (169), bamboo (98) and some highly branched trees, e.g., Cerberiopsis candelabrum (425) and Tachigalia versicolor (108) exhibit monocarpic habit.

Short life span of most monocarpic plants has been harnessed by scientists for basic physiological research. It is for this reason that the mechanism of whole plant

senescence has been studied in short-lived monocarpic plants such as soybean (24,72,73,89,294,295,299), pea (122,135,210,227,228), rice (30,31,32,257,259,339), wheat (35,39,151,237,318,323) etc. Study of senescence in intact plant is particularly important since detachment not only removes the organ from the normal influence of correlative controls, but may prevent the normal exodus of nutrients that may be released during the senescence process, thereby causing their accumulation and modifying the pattern of changes taking place at the cellular level.

Most of the works on monocarpism were done on annuals or biennials owing to a number of advantages. It is easier to monitor changes associated with the development of senescence in monocarpic annuals and to tackle the whole plant for experimental purpose with greater ease, compared with polycarpic plants or long-lived monocarpic plants.

An overwhelming body of research reports on monocarpic senescence has accumulated over the last two decades and they have been comprehensively dealt with in a number of excellent books and reviews published in recent years (64, 97, 183, 208, 283, 286,290,291,297,307,351,377,491,452,453, 454). The earlier reviews on this aspect are those of Molisch (253), Leopold et al.(210), Janick & Leopold (168), and Nooden & Leopold (291). A number of physiological and

biochemical changes takes place during ageing and senescence of a whole plant. A brief review of literature dealing with such changes will now follow.

1.3. Physiological and biochemical changes associated with leaf senescence :

1.3.1. Changes in photosynthesis and respiration :

During monocarpic senescence the leaves show a decrease in a wide range of physiological functions (281,291,410) and among them the decline in photosynthesis is the most important. The rate of photosynthesis gradually declines in attached and detached leaves during senescence of several species (117,220,221,271,397,452,456). It is well known that during senescence photosynthetic pigments are gradually degraded, but several workers have suggested that chlorophyll degradation is not directly correlated with the decline in photosynthesis during senescence (221,449). This is now strongly supported by the mutant of Festuca pratensis, where senescence occurs without chlorophyll degradation. Nooden (284) has concluded that photosynthetic capacity depends on the concerted actions of light and dark reactions. The degeneration of rubisco and other stromal enzymes during senescence is the important factor for declining photosynthesis (138,221,224,323,397,442). However, some reports indicate that rubisco activity may not be correlated with the decline

in photosynthesis (53,369,445). Along with the CO_2 fixing enzymes the rate of photosynthesis is greatly determined by ATP forming reaction or photophosphorylation, which declines during senescence (170,410). The rate of photosynthesis is modulated by supplying nutrients (310), water status (261) or by hormones (336,378) and removal of active sink organs, which greatly delays monocarpic senescence, but not in all species (8,65).

Senescence is an active, ATP requiring deteriorative process, and the respiratory activity is sustained till very late stage of senescence (291,345), increasing thereafter (364,401). Climacteric rise in respiration has been noticed during senescence of flowers and fruits (142), and in leaves (4). It may be assumed that the sustaining respiration during senescence serves to synthesizing catabolic enzymes (354) and also to export the resulting materials from the senescing tissue (297). During senescence of detached leaves, the respiratory quotient remains low, which indicates the combustion of amino acids produced from protein hydrolysis (351). ABA and BA promote and inhibit respiration and uptake of inorganic phosphorus, respectively, through uncoupling and coupling of oxidative phosphorylation (246,364,381).

1.3.2. Changes in nucleic acids and protein during senescence :

Nucleic acid and protein, two most important biomolecules, do regulate most of the physiological and biochemical processes in plants. DNA content decreases during senescence in both attached and detached leaves of several species (43, 55, 94, 145, 420). However, opposite reports are also available (16, 225). It has been also reported that the number of copies of DNA in plastome declines during senescence (199, 367), which may be the actual cause of decline in DNA in the leaf tissue during senescence (197). Chang et al. (55) have observed that the repetitive sequence of DNA of cotyledonary nuclei declines during senescence, while the other region remains intact.

The total RNA content in the leaf tissue declines during senescence of several plants (30, 281, 291, 410). The different types of RNA present in the cell are degraded in different times and at different rates. Thus, m-RNA synthesis declines during senescence of oat leaves, but some new m-RNA reappears (226) and those are present in the senescent cells behave quite differently from the early stages in the nature of translation (437). The increase or decrease in the abundance of t-RNA depends on the growth stage and physiological activity (326) and also in the nature of acetylation (327). The chloroplast RNA is selectively degraded during senescence of Perilla, cucumber and tobacco leaves (51, 52, 398). The loss

in RNA is due to increase in RNase activity in detached leaves (88,115), but such correlation between RNA level and RNase activity was not observed in attached leaves (194,291).

The breakdown of protein is the characteristic feature and universal during senescence of cells, organs, or organisms (198,223,281,289,444). Such ^{an} event, however, may be delayed by supplying nutrients, hormones or by several surgical treatments, having delaying effect on senescence (99,223,443) in some, but not in all species (65,137). Most of the works have been done on leaf soluble protein, rubisco, which greatly declines during senescence (112,222,443). Also, the loss of membrane protein and cytochrome are reported (50,347,408). Several reports suggest that the loss in protein is due to concomitant increase in protease activity (27,234,438), ^{but} Mae and Ohira (219) have observed no such relationship in rice plant. Veierskov and Thimann (424) have suggested that loss in protein is due to impairment of vacuolar membrane which allows the protease to attack in the cytosol and organelles.

It is now known that leaf senescence requires the synthesis of specific senescence proteins in the cytoplasm (410) and in the chloroplast (79,80,352,460). Chloroplasts isolated from attached senescent leaves synthesize almost exclusively several proteins that are different from those

synthesized in young leaves (114). Significantly, the inhibition of chloroplast protein synthesis retards the loss of chlorophyll and protein by senescent leaves (80, 236). However, just before leaf senescence there is an increase in the protein synthesis in chloroplasts (114,236). Martin and Sabater (235) have shown that kinetin controls chloroplast gene expression in senescent leaves at both the transcriptional and translational levels. Further studies indicate that early in senescence, the polypeptides of the envelope change, but that probably most of the new polypeptides are synthesized in the cytoplasm (136). The results of Guera et al.(136) further indicate association between the thylakoids and many of the proteins synthesized by senescent chloroplasts, which may be related to subsequent membrane lipid and pigment breakdown (454). According to Thimann (406) proteins that retard senescence are different from those which accelerate it.

Chromatin-associated histone and nonhistone proteins are also important in the regulation of gene action (191, 316,388). Petel and Berlyan (317) have observed a close relationship between DNA/histone ratio and RNA content. Decrease in HI histone has been correlated with transcriptionally poised chromatin structure (69). More subtle tissue-specific shifts in the ratio of histone variants have been demonstrated in numerous cases (186,279,388,433).

1.4. Ultrastructural changes in the leaf tissue during senescence :

The deterioration at the ultrastructural level of chloroplast^s, mitochondria and membrane has been observed during senescence. The degeneration of chloroplast has been reported in several species (28,117,454,455) and thought to be mediated by hydrolytic enzymes (83,238). Several reports suggest that the number of chloroplast_s decreases during senescence (199,443), whilst others indicate that it remains constant till very late stage of senescence as in wheat and barley (238,434). The stroma thylakoid is degenerated before grana thylakoid (133,280,409), which is evident from non-yellowing mutant of Festuca (408). The gradual increase in osmophilic granules in chloroplast is observed in several species (133,280,323,445) due to degeneration of thylakoid. Lastly, the envelope of the chloroplast is disrupted after complete deterioration of internal membrane system (144,455).

The mitochondria are more stable than the other cell organelles and their structural integrity is lost in the very late stage of senescence (214,345,348). The molecular events suggest that dismantling of mitochondrial membrane may be initiated by internal selective proteolytic enzymes, possibly triggered by conformational changes in the membrane protein. The protease attack on the membrane liberates amino acids which may possibly be the cause of sudden rise in respiration prior to senescence (348,455).

The most notable feature of senescence is the deterioration of microsomal membrane resulting in loss of permeability and selectivity (90,244,411,413), which permits the release of substrates, cofactors, ions and hydrolytic enzymes and disrupt the compartmentalization in the cell. Such events enhance the dysfunction of cell or tissue. Three main causes of membrane dysfunctions are : (i) change in phase properties from liquid-crystalline to gel-crystalline phase, (ii) formation of bilayer lipid configuration, and (iii) specifically inverted micelles (244,411).

The coexistence of both phases alters the pattern of protein organization, affecting enzymes (361) and renders lipid bilayer highly permeable (15). Electron spin resonance (ESR) and fluorescent depolarization studies of isolated membranes from senescing tissue showed decrease in lipid fluidity (244,412). The fat or fatty acids of membranes are also lost during senescence (58) due to increase in phospholipase activity. From such fatty acids, jasmonic acid, a highly senescence promoting agent (362) and malondialdehyde, a fatty acid degradation product (196,400), are produced which are increased during senescence (177,319). Membrane protein degradation is also an important feature of dismantling of membrane. The number of thiol groups per unit membrane protein declines during senescence or there occurs a selective loss in thiol-rich proteins (244).

1.5. Correlative control of whole plant senescence :

The different organs of plant form a complex system which influences each other in a way that serves to achieve a coordination of developmental processes (17,127,355). A branch on a tree eventually dies along with the tree, but if excised and rooted the branch becomes a full grown tree. Also the longevity of leaves is greatly extended by excision followed by rooting (59,253). In tissue culture, any cell of a plant forms a new plant by nutrient and a balance of hormone application. Thus, the genetic constituents are same in every cell, but selectively expressed by hormones produced by different plant parts, which also regulate mobilization of nutrients and physiological functions. Thus, all the organs are interlinked and they regulate functions of the whole plant in a correlative manner. Correlative control also operates at the cellular level (17), the prime case is the xylem differentiation (380).

Most successful approach to analyse correlative control has been the surgical methods. The excision of one organ permits the analysis of its effects on the other. It has been observed that pollination enhances senescence of petals within a very short time (128,253), but inhibits degeneration of ovary. In germinating seeds, cotyledons deteriorate due to supplying of nutrients to the shoot apex. Thus, removal of shoot apex delays cotyledon senescence (26,270). The removal of roots promotes senescence

of leaves (284,432). Also, within a leaf the petiole may promote blade senescence and its removal extends the life-span of excised betel and Hibiscus leaves (248,251). In soybean, bean, rice and many other plants removal of reproductive structures retards senescence (257,289,291,421) but not in all species (8,65,137).

Shoot systems are more important in regulating whole plant senescence; the plant dies because the assimilatory organs senesce (282). This is strongly evident from the photoperiodic manipulation and root/shoot grafting experiments (282). Thus, it appears that supply of nutrients and hormones from leaves and roots is the prime factor in regulating whole plant senescence. The retardation of senescence by cytokinins, xylem differentiation by auxin, ABA dependent stomatal closure and regulation of root growth by auxin (288,452) suggest that hormones actually regulate all the physiological processes of whole plant as well as its senescence (32,127,209,339,435). Ambler et al. (10) have showedⁿ that nonsenescent Sorghum exhibits delayed leaf senescence due to correlative controls between root-produced hormones and shoot development. ^{On the other hand} (And) nonsenescent Sorghum showed higher level of cytokinin (9).

From the available literature it becomes apparent that senescence of monocarpic plants is more amenable to analysis than senescence of polycarpic plants and therefore, we know

a great deal about monocarpic senescence. In most of the cases but not always, the fruits, particularly the seeds, have been shown to induce monocarpic senescence. A wide range of degenerative changes occur during monocarpic senescence, and, as already described, changes in one part of the plant induce alterations of other parts of the plant. In most monocarpic plants, the decline in leaf function and shedding of the leaves seem to be particularly important. The correlative effects, e.g., seed effects on the leaves, may be mediated by hormones as well as other factors (97, 290). Many attempts have been made since the time of Molisch (253) to explain the mechanism of monocarpic senescence. But up to date no singular theory seems to be appropriate and satisfactory enough to explain the general phenomenon of this terminal developmental process, especially the triggering mechanism of the process.

Since the most remarkable phenomenon is the post-reproductive senescence of the whole plant, i.e., monocarpic senescence, we will discuss the present concept of the mechanism of monocarpism.

1.6. Theories of monocarpic senescence :

Current reviews on plant senescence reveal that, although a large number of studies on monocarpic senescence of plants have been carried out, the actual mechanism of this process

is still far from clear and it appears that the process is very much complex (64,97,183,208,209,210,281,283,289,290,297,307,351,452,453). It also becomes fairly clear from the perusal of these reviews that there exists considerable discordance among scientists with regard to the mechanism of senescence in monocarpic plants. Admittedly, one thing appears certain that it is not merely a time dependent uncontrolled process, but a very much regulated self-destruction process, where a dramatic degeneration occurs in an orderly fashion following the reproductive development dictated by the genetic programming of the species concerned.

Various proposals have since been put forward to explain the mechanism of monocarpic senescence, which can be grouped under the following four hypotheses : (i) the nutrient drain hypothesis, (ii) the production of death signal by reproductive structures, (iii) the hormonal regulation of whole plant senescence, and (iv) the nutrient stress-induced hormonal disbalance leading to senescence. The available experimental evidence in support of each hypothesis will be cited and the relative merits and demerits of each hypothesis will be discussed in the pages to follow. It may be mentioned here that not a single hypothesis does provide sufficient proofs for elucidating the actual mechanism and each has got its own limitations.

1.6.1. (1) Nutrient drain hypothesis :

This hypothesis, put forward by Molisch (253), suggests that mobilization and drawing of nutrients and organic compounds from the vegetative parts (photosynthate from the leaves and hormones and nutrients from the roots) by the reproductive parts cause monocarpic senescence. According to this hypothesis a pull from the strong sink of young reproductive tissues monopolizes all nutrients, helped by a reduced sink strength of the vegetative parts of flowering plants. This hypothesis has recently been modified by Kelly and Davies (183) and has received renewed attention in recent years (139,182).

Working with G-2 line (photoperiod-sensitive) of Pisum sativum, Peter Davies and his coworkers (122,139,140,141,182) made significant contributions to our understanding of the influence of the reproductive structures on monocarpic senescence. In this genetic line, senescence does not occur in short-day (SD) despite fruit production and the accompanying nutrient drain to the fruits, which may be as great under nonsenescing as under senescing conditions. They have recently demonstrated that the rate of reproductive development as well as senescence are regulated by interaction of genes (Sn and Hr) and photoperiod (181). They have argued that delay of senescence in SD is due to reduced sink demand of the developing reproductive structures for

assimilates, resulting in more assimilates available for vegetative growth. The correlation of delayed apical senescence and greater assimilate supply to the vegetative structures has been demonstrated by Kelly and Davies (182). This observation supports some aspects of Molisch's proposal that fruits or seeds divert assimilates from the vegetative parts, triggering their senescence, when they received insufficient assimilates to survive.

Both the nutrient drain hypothesis and a hypothesis in which it is proposed that the reproductive structures produce and export a senescence signal (281), assign a central senescence-inducing role to fruits or seeds, no doubt, due to the observations that removal of reproductive structures delays or prevents senescence of many species (289). However, senescence of peas (343) and other species (289) has been reported in the absence of fruits, and argues against a central senescence inducing role for fruits and seeds. Moreover, in soybean, early senescence-like changes and loss of assimilatory capacity were independent of the presence of fruits (47,74). These observations speculated that senescence was induced early in the reproductive phase, and was only enhanced by the fruits. The results provided by Kelly and Davies (182) also supported this conclusion. The effects of the senescence controlling genes were apparent on assimilate partitioning with⁻ⁱⁿ the apical bud of G-2 peas,

long before fruits or seeds were present. It seems likely that these genes mediate partitioning between primordia, very early in reproductive development. Furthermore, root growth (359) and assimilation by roots (202) have been found to decline before the period of rapid pod growth in pea which indicates decline in the sink strength of the vegetative parts, which is associated with flowering, while the ability of reproductive sinks to divert assimilates regulates senescence. Kelly and Davies (182) further suggest^{ed} that this ability is conferred on reproductive sinks by, and regulated by, the whole plant, starting early in the reproductive phase. Providing different lines of evidence from experiments on rice plant, Choudhuri and Mondal (64) have suggested that senescence-inducing genes are expressed at the time when floral differentiation takes place.

The current works of Hamilton and Davies (139) on the quantitative export from fruits (140) and the identification of the exported materials from the fruits as sucrose and malic acid, have led them to abandon the concept of senescence factor or signal. According to them the shift in nutrition partitioning that is diverting more photosynthate and nutrients to developing reproductive structures, causes less nutrients available for continuing vegetative growth. As seeds develop, the nutrient demand of the seeds leads to the further reduction in nutrients available for continued growth. Although this is not the cause of senescence, it

magnifies the already existing nutrient depletion of vegetative tissue, so that senescence takes place. It seems that the mechanisms of monocarpic senescence are probably not the same in various plants, with small differences between the species and large differences between the plant families.

1.6.1.1. Sink strength, mobilization and senescence :

The conspicuous growth of the reproductive apices after being transformed from vegetative apices, seemingly at the expense of the vegetative structures, and the close correlation between seed-filling and monocarpic senescence, lend credence to the concept that death is a consequence of exhaustion and starvation due to a massive export of nutrients to the developing fruits (32,35,39,253,259,339,383). It is observed that senescence in mature plant parts is influenced or enhanced by young growing organs (320,283,341). As the individual leaf develops and ages, they switch over from net importer of metabolites to net exporter (419). It is now well recognised that source-sink interactions are complex, because the plant may adjust itself as normal development progresses or in response to experimental manipulations (75,116,161,290). In particular, removal of reproductive structures not only eliminates sinks and may delay senescence, but may also allow alternative sinks to replace those removed (338,340,399). Nonetheless, sink demand usually can influence the assimilatory

metabolism of supplier organs. Earlier recognition of the differences among species and the variety of possible responses to source-sink alterations could have avoided much unnecessary disagreement (290).

Adjustment of photosynthesis to sink demand has been seen in many plants (290). This might be achieved through changes in stomatal or mesophyll conductance, over the short and long term, respectively, which may be mediated by ABA. Normally ABA produced in the leaves flows to the fruits. Hence, fruit removal causes ABA level to rise in leaves, stomata to close (188, 189, 373) and the photosynthetic ^amechanism to decrease in the leaf blades of many plants (337). While a decrease in photosynthetic rate in a normal plant is the senescence syndrome in monocarpic plants (287), it may not accurately reflect senescence or it may be also influenced by diminishing sink demand. The decline in photosynthesis, which results from the loss of photosynthetic components (chlorophyll and RUBP case) rather than the effects of sink loss, may better reflect monocarpic senescence (289).

Although the redistribution of mineral nutrients from leaves to developing fruits, particularly in monocarpic plants, is the most striking example of redistribution, exactly what regulates this is uncertain. Contrary to expectations, redistribution, even for mobile nutrients such as

phosphorus and nitrogen, may be inhibited by a deficiency in these elements or promoted by an abundant supply (281). The experiments conducted by a large number of workers suggest that interplay between the sinks (developing fruits) and the sources (vegetative parts, especially leaves) is more complex than a simple withdrawal. However, the observations that fruits act as a powerful sink by virtue of their higher hormonal level (48,76,84,85) than the leaves or other vegetative parts resulting in preference of movement of metabolites to the reproductive structures, seems to strengthen the idea of nutrient drain hypothesis. Although fruit development influences the allocation of nutrients, the possibility that root growth may be controlled by factor(s) other than metabolite supply from the shoot cannot be ruled out either.

1.6.1.2. Stomatal conductance, reduced transpiration, mobilization and senescence :

Stomata regulate CO₂ exchange rates as well as transpiratory water loss. Stomatal conductance decreases with ageing, which in turn, reduces photosynthesis and transpiration (112,374,444). The xylem flux, in general, is controlled by stomatal aperture which may, in turn, control transpiration (289). However, in unstressed plant, stomatal resistance does not increase markedly until quite late, that is, after redistribution has progressed quite far and yellowing is about to

start (115,284) and, therefore, is unlikely to regulate xylem flux as a prelude to monocarpic senescence. Several studies have shown that the inhibition or acceleration of leaf senescence is paralleled by changes in stomatal aperture (315,403,404,407). Interestingly, cytokinin promotes stomatal opening and retards senescence, whilst ABA produces opposite effect (115,160,171,403). It is also in record that guard cells remain viable and functional even when the mesophyll cells are senesced (115,149,159,161). According to some authors, the stomatal movement is controlled by factors external to the guard cells (149,311). This speaks against stomatal regulation of senescence. Another interesting observation is that defruiting of wheat decreases stomatal conductance, but inhibits leaf senescence (41), which may be an ABA effect (215,373). Furthermore, Garrison et al.(115) have suggested that rising stomatal resistance in maturing unstressed soybean is rather a late event and may not be associated with the initiation of senescence, since defruiting causes at least a partial stomatal closure in soybeans yet inhibiting monocarpic senescence (212,215). Hurng et al.(159) have also demonstrated that stomatal closure is not directly proportional to aging of rice leaf and that guard cells tend to live longer than mesophyll cells. Since, stomatal closure may actually accompany delayed senescence in intact plants, other factors appear to be involved.

1.6.1.3. Vascular architecture, mobilization and senescence :

The vascular tissue (xylem and phloem) of monocarpic plants plays a significant role in the mobilization of photosynthate from the leaves, and water, mineral nutrients and hormones from the roots. The work of Neumann and Nooden (275) indicates that excision of seeds does not prevent translocation of [^{32}P]-phosphate out of the leaves, but transported more in the stem and petiole instead of pods. Thus, the vascular architecture seems to impose a preferential pattern of translocation rather than an absolute restriction on movement. The destruction by heat girdling of the phloem in the petiole of the target leaf, a treatment which blocks withdrawal of nutrients from the blades, does not prevent the nearby pods from inducing senescence of that leaf (295). In fact, the pod causes senescence of the leaves; however, supplying high level of mineral nutrients and cytokinin through the xylem may override the action of the pods (115, 276, 278, 284). Thus, it appears that a decline in the flux of minerals and cytokinins from the roots via the xylem is necessary for the pod to induce senescence (294).

Although depodding and phloem destruction in the petiole prevent exodus of the foliar nutrients, there seems to be some breakdown of foliar protein and resynthesis of other proteins in cells along the veins (109). This further suggests that hydraulic conductivity and the architecture of the xylem

are important factors, perhaps more important than stomatal resistance, in determining partitioning via the xylem (269, 462). Martin (237) has observed that stem xylem is a possible pathway for mineral retranslocation from the senescing leaves to the ear in wheat. He has suggested that a continuous connection by sieve elements between leaves and grains in wheat is not a prerequisite for mineral retranslocation. Although, the arrangement of vascular tissue determines redistribution of solutes, the structure of transport system itself does not control, even though it may favour, the movement from source to sink (247).

Orthostichous connections may restrict translocation of photosynthate from leaves to fruits. Although very little is known about orthostichous restriction of hormone movement, the information on nutrient flux must also apply to other regulatory factors which move in the vascular system (269). Recognizing and analysing these connections seem essential for understanding the mechanisms by which whole plants coordinate the activities of their parts including monocarpic senescence. Thus, it appears that although nutrient redistribution may be a function of senescence, it may not necessarily be the cause of monocarpic senescence.

1.6.1.4. Control of senescence by nutrients :

If mineral deficiency is one of the factors controlling senescence, it is expected that applications by foliar spraying of minerals could retard senescence. In fact, foliar spraying of nitrogen (33,42), potassium (363), calcium (328), boron (29) and manganese (33) have been found to retard leaf senescence. Interestingly, some nonessential elements, such as nickel (250) and cobalt (417) also retard leaf senescence. In several cases these mineral elements have been found to alter the endogenous hormonal levels (201,358,365). Some contradictory effects have, however, been reported; neither application of NPK to soybean leaf surfaces (372) nor force-feeding via the xylem (242) prevented loss of these minerals from the leaves. Similarly, foliar application of urea did not retard chlorophyll loss in corn (23). All these observations point out that inorganic nutrients may regulate senescence indirectly possibly by modulating endogenous hormonal status, particularly cytokinins, or changing enzyme activities, or both.

1.6.1.5. Criticisms against nutrient drain hypothesis :

The nutrient withdrawal theory of senescence has, however, been questioned for some time (210,263,264,281,283,289,291, 297,299). Thus, in several dioecious plants such as hemp (Cannabis sativa) and spinach (Spinacea oleracea), the male plants senesce much like the female plants, even though they

do not form flowers and seeds and can, therefore, account for only a limited nutrient drain to the reproductive structures of the plant (210,264). It is also possible to induce spinach plant to bolt by treating the plant with gibberellic acid under short days forming a tall leafy shoot (a massive sink) which does not form flowers. These plants do not senesce if not allowed to form flowers and seeds (168). In maize, the removal of reproductive parts may accelerate senescence (8,65). Similar observations were also made in oat (230) and Capsicum (137).

Fruit excision has been reported to increase endogenous ABA level and stomatal resistance (215,374), which may be one of the reasons for early senescence in these plants. Krizek et al.(190) have shown that cocklebur senesces and dies if the flower buds, formed under short days, are removed. Thus, in this plant photoperiod-induced flowering rather than seed development seems to control senescence.

Although removal of reproductive structures prevents rapid death of many plants, such as soybean, pea, bean, wheat, rice etc., many physiological and biochemical changes, generally associated with senescence, are not prevented (289). Decapitation of reproductive structures in male as well as female hemp and spinach plants delay^{cel} senescence (71,210). Graft^{ing} experiments or photoperiod manipulation in soybean and pea strongly suggest that the leaves and not the roots

or even the stem, appear to be the primary target of the influence exerted by the reproductive structures in many monocarpic plants (213,229).

Further evidence contradicting nutrient drain hypothesis comes from the interbreeding experiments with pea cultivars. Thus, it is possible to obtain recombinants which do not undergo normal senescence and death following seed production (239). The most significant contributions contradicting nutrient drain hypothesis have come from the work of Nooden and his coworkers at the University of Michigan. They found that monocarpic senescence in soybean was independent of pod number (sink size) over a very wide range (213,299). Subsequently, three lines of evidence based on very different approaches have shown that the nutritional requirements of the developing soybean seeds can be satisfied without sacrificing the plant if the assimilatory capacities are maintained. The first line of evidence can be provided from surgical experiments, that take advantage of the limited mobility of the senescence signal, which show that when the plants are modified so that the leaves are not contiguous to the pods, the latter can develop without killing the feeder leaves (213,282,299). Despite the criticisms made by Woolhouse and his coworkers (377,431), these experiments conducted by Nooden and his coworkers, do separate seed development and leaf senescence. It was

also shown by Nooden et al.(299) that reduction of pod number also reduced seed dry weight and N accumulation roughly proportionately. Thus, the idea that dominant reproductive structures compete through a simple passive sink effects on nutritional flux, does not seem to hold good. The second line of evidence against this hypothesis is a nonsenescent mutant of soybean which seems to produce a normal load of pods without the usual breakdown of the plant's assimilatory apparatus (3). The third line of evidence provided by Nooden et al.(298) shows that foliar spray treatments with combination of auxin and cytokinin can override the senescence signal and prevent monocarpic senescence. Moreover, 'sink demand' does not correlate well with monocarpic senescence when different species are compared (383).

Taking advantage of the photoperiod control of monocarpic senescence in G-2 peas independent of pod development, Gianfagna and Davies (122) have shown that nutrient demand by the seeds does not in itself cause monocarpic senescence. Thus, from these results nutrient diversion does not seem to be a primary trigger of monocarpic senescence. Although the exact role of nutrient deficiency in senescence, whether by withdrawal or diversion, is not clear, it can be argued that nutrient deprivation plays a role as an important background factor (281,283,295).

1.6.2. (ii) Production of death signal by reproductive structures :

From the discussions made above one is tempted to think that there exists some mechanism by which reproductive structures act on the vegetative parts, particularly the leaves, and this influence has been termed as 'senescence signal' by Lindoo and Nooden (213) and 'death hormone' by Nooden and Leopold (291). This hypothesis proposes that a senescence factor, probably hormonal in nature, originates in the seeds and migrates to the leaves inducing their senescence. The postulation for a control mechanism of monocarpic senescence mediated by a 'death hormone' is strongly favoured by Nooden and his coworkers working with soybean (281,283,291,297). The first idea of signal hypothesis perhaps comes from the works of Leopold et al.(210) and Janick and Leopold (168) with spinach plant. The source of the signal according to these authors is the seed in most, but not all, of the monocarpic plants. However, little information is available on the behaviour of 'senescence signal' in species other than soybean.

The exertion of the influence of senescence signal seems to occur during very late pod fill in soybean; depodding even quite late in pod fill still prevented the rapid yellowing and quick death of the plant (213,299).

The movement of the senescence signal is restricted, though clearly less constrained than the nutrients that support pod development, for monocarpic senescence. Nooden et al. (299) have also provided evidence that pod development can be uncoupled from senescence.

It has also been shown that the senescence signal exerted mainly on the leaves closest to an individual pod or pod cluster (281). Beyond this, the senescence signal seems to travel mainly downward, but stays within the same orthostichy as the source pod (213,281). The main influence, that on the nearest leaf, is not blocked by steam girdling of the petiole thereby indicating that it is exerted via the xylem (284,295). However, the fact that the signal moving downward is blocked by steam girdling of stem suggests that it moves downward via the phloem.

Several criticisms of their findings have been offered by Wang and Woolhouse (431) and Sexton and Woolhouse (377). However, these have been recently refuted by Nooden (289). It has been suggested (289) that the senescence signal differs from florigen. Earlier works of Davies and his coworkers on the apical senescence of pea (86,121-123) have suggested the downward movement of senescence-inducing substance from the fruit to the apex. As already stated they are of different opinion now and conclusions derived from their recent studies with pea support the nutrient

diversion theory. Kulkarni and Schawabe (193) have shown a different transmissible senescence-inducing factor which originates in the leaves of Kleinia articulata induced by long-day photoperiod. This influence is less mobile than the senescence signal of soybean. In an interesting study with groundnut, Ghosh and Biswas (120) have provided evidence in support of the senescence signal coming from the aerial flowers which do not bear fruits. The removal of aerial flowers caused lesser senescence in groundnut than that of fruits developed from cleistogamous flowers, suggesting that the aerial flowers exert more lethal effect on the senescence than the fruits/seeds produced by the cleistogamous flowers.

Assuming that neither ABA nor ethylene are death hormone per se (292), little is known about the possible identity of the putative death hormone. The case for a 'pea factor' with a carboxyl group was weakened when the compound was found to be sucrose and malic acid (139). Besides ethylene and ABA, the other naturally occurring compounds, in at least pea and soybean, with characteristics of death hormone, are chloroindole auxin and jasmonic acid (97).

Thus, most of the available evidence support both 'death hormone' and 'nutrient drain' hypothesis, although each cannot explain the mechanism of senescence in all monocarpic plants. With the development of new and sophisticated techniques, the riddle of death hormone may be resolved in the years to come.

1.6.3. (iii) Hormonal regulation of whole plant senescence :

It is now becoming increasingly clear that senescence involves a shift in the balance of senescence promoting and senescence retarding hormones. Most of the plant hormones have been implicated in senescence and each one has been shown to have regulatory power over the development of this syndrome (289,351,403,453). Although a plethora of research reports is available to substantiate the view that hormones control the senescence process, the exact role played by the known hormones in triggering senescence is far from clear. Sabater (351) holds the view that plants have possibly evolved mechanisms for the control of senescence by hormones as they have evolved mechanisms for the hormonal control of their correlative development according to their genetic potentialities and to the changing necessities of the plant.

In order to assess the hormonal control of senescence one must know those hormones which affect senescence symptoms; changes in the endogenous concentration of the particular hormone during senescence and changes in tissue sensitivity of the particular hormone. The causative relationship between senescent organs induced by change in hormonal level and the observed symptoms of senescence must be established. Although a great deal of information on the hormone effects of senescence of detached leaves is

available, our knowledge on changes in hormonal level and correlative effects among organs of the whole plant is fragmentary.

There are a number of reports which indicate that endogenous level of auxin decreases with leaf age. Production of auxin by the leaf blade and a decline in the flux of auxin down the petiole have long been implicated in the control of leaf abscission (281). However, very little effort has been made to understand translocation or changes in endogenous level of this senescence regulator in soybean. The ability of the auxin transport inhibitor, triiodobenzoic acid, to increase the number of pods in soybean suggests that the auxin may be involved (113,152). It could be that auxin mediates the inhibitory effect of young pods on subsequent pod initiation (158). Treatment with auxin, especially the synthetic auxin, α -naphthalene acetic acid (NAA), delays monocarpic senescence of soybean (167). Interestingly, a combination of auxin, such as NAA and cytokinin, such as benzyladenine, dramatically prevented monocarpic senescence in soybean (298). The fact that auxin retards foliar senescence in some, but not all species (291,309,403) and that auxin exerts the opposite effect, that is promotion of senescence during induction of xylem formation (380), have made it a dubious candidate as a regulator of monocarpic senescence.

The endogenous level of gibberellin has been found to decrease with leaf age (60,107). Gibberellin may also be synthesized in roots and decreased level of it may accelerate leaf senescence. The application of gibberellin can also delay foliar senescence in many species, such as, Tropaeolum sp. (60), Taraxacum officinale (107), Rumex sps. (125,254) and Lemna trisulca (18). Apical senescence in peas is delayed by gibberellins (329). However, foliar application of gibberellic acid does not alter monocarpic senescence in soybean (281). In most of the cases where gibberellic acid retarding senescence, cytokinin is generally less effective. It may be that gibberellic acid substitutes for cytokinin in such species. Since the effect of gibberellic acid is very much limited in the control of whole plant senescence, its regulatory role on monocarpic senescence seems doubtful.

Among the senescence retarding hormones, cytokinins are the most clearly implicated hormone in senescence. Cytokinins have their effects in attached as well as in detached leaves (4,107,214,259,342,346). A variety of experimental approaches has provided compelling evidence that cytokinins can delay or even reverse senescence in excised organs, particularly in leaves, and these observations have strongly supported the contention that a reduction in endogenous concentration of cytokinin in leaves is an important factor

in the initiation of senescence (297,351,403). Although the effectiveness of exogenous cytokinin treatment on attached leaves is less clear, cytokinin in combination with auxin can inhibit the seed-induced senescence of leaves in intact soybean plant (281,298). Purohit (332) could reverse ethylene-induced senescence in sunflower by kinetin treatment. There are, however, a few exceptions of senescence retarding effects of cytokinins (265,309). These results indicate that there is certain diversity of the hormonal mechanisms controlling senescence. According to Sabater et al,(353), cytokinins affect different senescence-related processes (chlorophyll and phosphate loss) independently, which suggests that cytokinin may prevent leaf senescence through multiple actions.

Many studies have provided evidence for the roots as a major and possibly the sole source of cytokinin production (211, 422). This root-produced cytokinin is a major factor in sustaining the leaf longevity (184,192,281). Long ago it was shown that longevity of excised leaf is extended by the formation of roots on these leaves (59,253). Stressed roots or root removal caused a foliar yellowing which could be relieved by cytokinins (278,281). To implicate the hormones further in whole plant senescence, it has been demonstrated that the flux of cytokinins from the roots is relatively high during vegetative growth and relatively low

during reproductive phase (281,422). Sabater (351) has suggested that decreases in the level of cytokinin during leaf senescence might be due to: (i) an accelerated cytokinin metabolism in the leaves before senescence, (ii) an accelerated transport from leaves to the other structures, and (iii) a decrease in the supply of cytokinin from the roots. It has been rightly pointed out (451) that sufficient emphasis has not been given on the interplay of different parts of the whole plant and in particular, the profound changes in the growth and metabolic activities in the roots as the fruits develop.

Kao (175) has concluded that in soybean seedlings, the leaf senescence is caused by a competition among leaves for root cytokinins. In other species, however, removal of the terminal and axillary buds or of the flowers increased flux of cytokinins from the roots (21,68) suggesting that fruit removal does not simply cause the elimination of source of competition for cytokinins. Although changes in cytokinin level generally correspond the leaf senescence, no correlation has been found between decrease in the fruit cytokinin and leaf senescence in soybean (214). Conceivably, seeds do not compete with the leaves for the supply of cytokinin (293). This implies that root cytokinins are not possibly the primary causal factor in monocarpic senescence at least in soybean. This is further substantiated by the observation

that the leaves of depodded explant of soybean do not yellow even if cytokinin is not supplied (278); therefore, cytokinin deficiency per se does not trigger foliar yellowing in soybean.

Abscissic acid (ABA), the most studied hormone, plays a great role in promoting senescence of leaves. ABA treatment promotes senescence in detached leaves of many species (22,291,389,403), whilst it does not accelerate senescence in attached leaves of others (95,281). Lindoo and Nooden (214) have shown that ABA accelerates senescence of podded plant but surprisingly, not in depodded soybean. That the age of leaf is an important determinant of ABA action is evident from the works of Smith et al (386), who have demonstrated that ABA has no effect on young attached leaf, while accelerating senescence of mature attached leaf of cotton. Several groups of workers have observed that ABA-like activities in leaves increase during the period preceding visible yellowing (32,60,214,259,339,360). However, no consistent change in the ABA level has been found during the senescence of primary leaves of Phaseolus vulgaris and field-grown soybean (64,70). Other inconsistencies with ABA are: young leaf containing more ABA than mature green leaves (281), complete depodding (which prevents foliar senescence in soybean) increasing foliar ABA level (373), and failure of foliar ABA application to induce senescence of depodded soybean (214). According to Nooden (289), high levels of

senescence retarding hormones such as cytokinins, which counteract the ABA in the leaves of younger or depodded plants, could be a cause of these discrepancies.

Generally the leaves and not the roots are the primary source of ABA (429). However, ABA is likely to be produced in root cap which, in conjunction with IAA, perhaps modulates the root growth (451). According to Hartung (146) this ABA of root origin probably is not translocated to leaves. Reproductive structures generally show high level of ABA content (281). Interestingly, labelled ABA injected into the pods does not travel to the leaves in significant quantities at the time of senescence (296).

It is well known that stomatal closure and ABA level are closely associated in senescence. Depodding has been found to cause at least partial stomatal closure and accumulation of ABA in leaves (205,373,375), yet depodding can delay monocarpic senescence (299). Furthermore, Samet and Sinclair (360) have reported that ABA level increases in senescent leaves of soybean, after other processes have been initiated. Admittedly, ABA may not be the signal for monocarpic senescence at least in soybean. Still, ABA may play an important role in the senescence process of many other plants, may be in conjunction with other factors.

The role of ethylene as a regulator of abscission (291), flower senescence (243) and fruit ripening (344,379) is well established. With a few exceptions, the involvement of ethylene in leaf senescence is still not clear. The endogenous ethylene can hardly be a specific signal for senescence induction since ethylene is produced in every cell and may move from cell to cell by diffusion. It is also well known that external application of ethylene promotes leaf senescence. Although some reports are available which have related changes in ethylene in leaves with senescence (5-7,176,331,332), no consistent relationship has, however, been established between ethylene production and whole plant senescence. Furthermore, inhibitors of ethylene synthesis or action do not always prevent this event. A number of reports suggest that there is a great deal of interactions between ethylene and other phytohormones. Kao and Yang (176) have shown that ABA promotes senescence, but significantly decreases ethylene production, whereas, BA retards senescence but promotes ethylene production in detached leaves. Both IAA and kinetin synergistically stimulate ethylene production in the leaf discs of tobacco (6). Sabater (351) has rightly pointed out that little attention has been paid to the possible effect in senescence of the well known high synthesis of ethylene after cutting (2). Thus, it appears that endogenous ethylene

may play a role in senescence, presumably by interacting with other hormones participating in leaf senescence.

Summarising the hormonal effects on senescence, it seems plausible that the endogenous levels of various phytohormones differ in different species and even in cultivars (156), in different seasons, and also in leaves of different ages (64). Trewavas (418) has pointed out that altering the concentration of a growth substance is not the only potential regulatory mechanism in the control of plant development, but it is the actual sensitivity of tissues to growth substances which is an important determinant. This would explain why different groups of growth substances or metabolites elicit different responses in the same tissue or organ at any time. But there is no definite proof that any of the known plant growth regulators acts as translocating signal in senescence. Thus, it is suggested by Sabater (351) that it is more than one hormone, or the hormonal balance, which controls whole plant senescence.

A sentence from Trewavas (418)

Woolhouse (451) has suggested how interaction between organs may come to play in whole plant senescence. The vegetative plant produces growth substances, such as IAA and cytokinins, from the actively growing shoot and root apices. The action of these substances perpetuates the vegetative condition, But as the apex switches to differentiating flowers, this 'feedback loop', is broken.

Again, as the leaves mature, the supply of IAA from the apex is substantially reduced. This, in turn, diminishes the supply of cytokinins from the roots as their growth becomes less active. The general decline in regulators that promotes the vegetative condition is accompanied by an increase in regulators from the developing fruits. This will include factors, such as that associated with the expanding pods (senescence factor) and ethylene, which promote senescence. They will also further modulate the supply of regulators that promote the vegetative state, thus, bringing about rapid senescence. Osborne (307) has suggested that an array of growth promoting hormones, nutrients and growth suppressing hormones appear to act in concert to control the sequence of events in organ senescence and to signal the onset of total organism senescence leading to inevitable cell death. It seems, therefore, more likely that a balance of growth promoters and growth inhibitors rather than an individual hormone determines the signal to overall senescence. If, however, the senescence-inducing hormone is actually involved, it may not be one of the known hormones.

1.6.4. (iv) Nutrient stress-induced hormonal disbalance :

Monocarpic plants are characterized by either having all the vegetative apices transformed into determinate reproductive structures (e.g., cereals) or having

indeterminate reproductive structures (e.g., pea, soybean etc.). Senescence processes in the monocarpic plants may take place in different organs at different times. Depending upon the presence or absence of reproductive structures, leaves of monocarpic plants followed two types of senescence. Thus, in absence of reproductive structures, the individual rice leaf senesces basipetally, i.e., the apical segment senesces first and then the basal part (172), because the growth of rice leaf is controlled by a basal meristem where the apical cells are older than basal cells. Again, senescence of intact leaf gradually starts from the bottom leaf and then proceeds in an acropetal order along the stem axis (257,339). Similar patterns are also shown by other cereals, such as maize (102). Further, the older the leaf, the lower is the level of photosynthetic efficiency and overall protein and nucleic acid synthesis. The dominance of the young over the old is thereby established so that the older leaves inevitably senesce and die first.

Neumann and Stein (277) have suggested that internally programmed changes in the hydraulic architecture of the plant progressively diverts xylem-transported root supplies of nutrients and cytokinins from basal to more apical leaves and thus possibly regulates the progressive senescence of leaves from the base upwards. Fraser and Bidwell (110) have suggested that successive leaves of a plant complete their

growth at different times and thus, begin their gradual decline independently. Murayama (267) has demonstrated that the death of lower leaves in rice is caused by the migration of nutrients from lower to upper leaves. A similar situation is also observed in maize (45).

Working with rice, Ray and Choudhuri (341) have suggested that the young growing vegetative parts can act as strong mobilizing centres for withdrawal of metabolites from the older senescing organs. Conceivably, the withdrawal of metabolites and mineral nutrients from the older leaves by the younger growing parts may cause a nutrient deprivational stress resulting in a hormonal disbalance (particularly in cytokinin and ABA) in them which seems responsible for the development of leaf senescence. The works of Choudhuri and his coworkers from this laboratory have provided strong evidence in favour of this hypothesis (32,257,258,259,339,340). Later studies by Biswas and his coworkers have corroborated this from their work with various types of plants (35-39).

From the studies of sequential and nonsequential mode of leaf senescence behaviour (257-259), it may be argued that the earlier senescence of the flag leaf in Jaya and Ratna cultivars of rice might be due to its close proximity to the reproductive structures. Had the reproductive structures communicated a senescence signal to the vegetative parts,

then the non-sequential mode of senescence would have been a universal occurrence in rice and other cereals. But the existence of the sequential mode of senescence in Masuri and Kalojira cultivars of rice where the flag leaf senesces later than the older second leaf, notwithstanding the close proximity with the panicle, strongly speaks against the movement of senescence signal from the reproductive structures to the vegetative parts leading to their senescence. Further studies of Choudhuri and his coworkers suggest that the withdrawal of metabolites may not be directly responsible for the onset of senescence, rather it possibly creates a situation (nutrient exhaustion) that would make the leaf suffer a deprivational stress leading to a hormonal disbalance and eventually brings about senescence of the whole plant (64).

Combining all the facts together, Choudhuri and Mondal (64) have postulated a scheme of events to explain the possible mechanism of monocarpic senescence in rice. The scheme envisages that depletion of metabolites in leaves due to export to grains imposes a nutrient-deprivation stress in leaves leading to accumulation of ABA. This accumulation ensures stomatal closure resulting in decreased transpiration. This, in turn, reduces efflux of root cytokinin (162,163), which is further compounded by the reduced synthesis of cytokinin in roots during reproductive development of the

plants (21,384). Such a condition leads to an imbalance of hormones in favour of possible ABA to cytokinin ratio (along with senescence factor) that increases with the reproductive development of the plant. All these conditions favour the development of senescence syndrome and the plant eventually succumbs to death. The change in balance from synthesis to degradation can be viewed in cells of mature tissues as a progressive decline in maintenance turnover of the process of repair (307). But the most intriguing question remains as to what triggers this process ?

1.7. Possible triggering mechanism of monocarpic senescence :

It is clearly evident that the reproductive structures exert marked influence on the monocarpic senescence, but the actual triggering mechanism of the process still eludes us. According to Nooden (289) monocarpic senescence may be viewed in terms of a preparatory and a final phase. The former involves a decline or even cessation of vegetative growth that renews the assimilatory organs and other tissues. Decreased mineral uptake and cytokinin production by the roots may also be important components of the preparatory phase. The massive decrease in the assimilatory activities and the major redistribution of minerals invested in this metabolic machinery seems to be part of the final phase (289). Most of the available evidence fits both a death hormone hypothesis and a nutrient drain hypothesis (97). According to

Choudhuri and Mondal (64), although mobilization of nutrients from the leaves to the fruits appears to hasten senescence, the actual trigger for the same at the genetic level perhaps comes at the time of floral differentiation. This can be corroborated from the observations that the duration of reproductive phase of different rice cultivars is fairly constant and the longevity of the cultivars varies due to variation in duration of the vegetative phase. Furthermore, the delaying of senescence of the whole rice plant either by removal of panicle or by application of hormones or nutrients could never be extended beyond a week or a couple and the senescence of rice plant could be deferred for about six months by preventing flowering by subjecting the photoperiod-bound rice cultivar to an unfavourable photoperiod in the field. Wangermann (432) observed that Viola tricolor dies following flowering or fruiting, but could over-winter in the vegetative state if they did not flower. Osborne (307) reported that she could prevent senescence of Xanthium plant for as long as eight years by keeping it under unfavourable photoperiod. Likewise, prevention of flowering may allow monocarpic plants to reach a much greater size and age than normal. For example, avoiding the chilling required by cabbage and sugar beet prevents flowering, thereby allowing these plants to live more than two years and also to become very large (81,82). Under noninductive photoperiod,

soybean plants can be induced to last more than fifteen months (281). Thus, the flowering signal and not some influence from the fruits induce senescence. It may be mentioned here that apex senescence in pea may occur in the absence of flowering (343), but it has been argued by Nooden (289) that apex senescence and monocarpic senescence are different phenomena in the pea.

A number of dioecious plants show that the male plants senesce much like the female plants. The former dies after flowering even though they do not set fruits or seeds. All these observations strongly suggest that the induction of flowering actually triggers monocarpic senescence and that the formation of flowers and fruits is perhaps of secondary importance (321). As flowering is a prerequisite for all monocarpic senescence, it seems probable that the genes responsible for triggering monocarpic senescence being simultaneously expressed at the time of floral differentiation, and the senescence-inducing genes and flower-initiating genes are possibly linked together (64). However, the ultimate manifestation of the senescence syndrome may differ somewhat in different species. Sabater (351) has suggested that the transition from a hormonal equilibrium retarding senescence to another equilibrium stimulating senescence may be triggered by genes, including a marked change in the supply or in the synthesis of an individual hormone. However, the exact mechanism

of gene expression and the involvement of senescence signal remains to be explored and there is a very good reason to continue the research for death signal, although their existence is certainly not yet proven beyond reasonable doubt. Development of adequate techniques and refinements of the methods can hopefully solve the problems relating to the programmed self destruction process of the monocarpic plants in near future.

*** Chapter –II ***

Studies in monocarpic senescence of plants

INTRODUCTION

Monocarpy is very common in cultivated plants, especially in crop plants, such as cereals, which display the most dramatic form of overall senescence. The spectacular event, which never escapes one's attention, is the sudden and synchronized death of plants in a cereal crop-field just before harvest time. In rice and wheat and other cereals, all the vegetative apices are transformed into reproductive structures at the time of switching over from one developmental phase to the other (64). These plants seem to serve as good experimental materials for studying the mechanism of monocarpic senescence, because here the source and sink are distinctly delimited and amenable to surgical manipulations and their life-span is also reasonably short for studying various changes generally associated with monocarpic senescence. The most characteristic feature of rice and wheat, which were used in the present investigation as experimental materials, is a special leaf, called the 'flag leaf', which emerges as the last leaf during the reproductive development. ⁵⁵⁻⁵⁶⁻⁵⁷ But the senescence behaviour of this youngest leaf is variable in different rice cultivars (257). Another characteristic feature of rice cultivars is that when the panicle is removed from the plant, a side branch

develops at the axil of the second leaf which alters the source-sink relationship, as also the senescence behaviour of the plant (257,339). Interestingly, such development of side branch could not be observed in depanicled wheat plant and hence there is no alteration in source-sink relationship in wheat as observed in rice.

As already emphasized in the review of literature (Chapter-I), that although a great deal of research has been carried out to elucidate the mechanism of monocarpic senescence in different plants, the nature of the actual trigger of the process is still not very clear and the process appears to be very much complex. However, if one goes through the current literature on this subject one will come to the inevitable conclusion that at present there are two hypotheses which are competing with each other to offer tangible explanations for the cause and effect of monocarpic senescence (97). Although the 'senescence signal' or 'death hormone' hypothesis has been well established in soybean (289) and is suggestive in some other plants (34,123,193), its isolation, characterization and mode of action are still eluding us. The other proposal, i.e., nutrient drain hypothesis, did not receive much attention since its postulation by Molisch (253), until recently. The publications from this laboratory on the mechanism of monocarpic senescence in rice (32,257,339) provided ample evidence in favour of the latter hypothesis, but

surprisingly that did not attract attention of the scientists working in this area. With the recent publication by Peter Davies and his coworkers (139-141,182) refuting their earlier contention of the involvement of senescence factor (signal) in the regulation of monocarpic senescence of pea, the pendulum now seems to have started swinging back to the nutrient drain hypothesis. In a recent review, Choudhuri and Mondal (64) have postulated from a number of experimental evidence that the genes responsible for inducing monocarpic senescence are probably expressed at the time of floral differentiation. It is interesting to record that the flowering process is the common prerequisite for inducing overall senescence in all types of monocarpic plants. The development of fruits rather increases the sink demand, thereby depleting leaves of their nutrients and accentuating the death of the whole plant.

In the present investigation attempts were made to study various physiological, biochemical, hormonal and anatomical parameters in a few rice and wheat cultivars showing variations in their patterns of senescence during reproductive development, which may offer explanations to the divergent patterns of senescence, particularly in some rice cultivars. Furthermore, the correlative control of the process, and the relative role played by the reproductive structures were also analysed by altering the reproductive development

by various physical and chemical manipulative treatments of the reproductive structures, particularly in rice cultivars. All these data embodied in the present thesis and those published in the literature in respect of the whole plant senescence taken together may lead to a proposition which will hopefully throw light on when and how the induction of senescence in monocarpic plants is triggered and the role played by reproductive structures in such an event.

MATERIALS AND METHODS

2.2.1. Plant materials :

Several cultivars of rice (Oryza sativa L.) and wheat (Triticum aestivum L.), which are widely used as staple food throughout the world, were selected as experimental materials for the present investigation. The rice plant is semiaquatic in nature, whereas the wheat plant is totally terrestrial. Both the plants are monocarpic, belonging to the family Poaceae under the order Glumiflorae. In India, rice is cultivated from 8° - 30° N latitude and under widely varying conditions of rainfall, altitude and climatic conditions. The rice plants are divided into two groups based on the response of photoperiod to flowering; photoperiod-sensitive (season-bound) and photoperiod-insensitive, the latter is grown regardless of seasons. Wheat plants are mainly grown in the tropical and temperate regions between 30° - 60° N and 25° - 40° S. The optimum temperature is about 25°C and annual precipitation ranges from 63-88 cm. In India wheat plant is mainly cultivated in Panjab, Haryana, Uttar Pradesh, Madhya Pradesh and Bihar.

For analysing the pattern and mechanism of monocarpic senescence, six commonly grown rice cultivars namely, Rasi

(IET 1444), Sashyasri, Kalojira, Badsabhog, Patnai and Kalma and two wheat cultivars, Sonalika and Kalyansona were taken as experimental materials. Of these six rice cultivars, Rasi and Sashyasri are short-statured and photoperiod-insensitive (grown in the dry season), Kalojira and Badsabhog are medium-statured and photoperiod-sensitive and Patnai and Kalma are tall-statured and photoperiod-sensitive (grown in the wet season).

2.2.1.1. Developmental stages of rice and wheat cultivars :

Rasi and Sashyasri rice cultivars have a good tillering habit, attaining an average height of 79-82 cm. Anthesis of these two cultivars takes place at the plant age of 94 and 82 days, respectively and crops are harvested after 133 and 122 days. Kalojira and Badsabhog have tillering habit lower than the short cultivars and their average height is 101-105 cm. Anthesis takes place at the plant age of 112 and 115 days, respectively and crops are harvested after 152 and 156 days. The tall cultivars Patnai and Kalma have good tillering habit, their average height is 118-121 cm and anthesis takes place at the plant age of 120 and 118 days, respectively. Crops are generally harvested after 163 days. Of the two wheat cultivars studied, Kalyansona has greater tillering habit than Sonalika; anthesis takes place at the plant age of 56 and 64 days, respectively and crops are harvested after 98 and 105 days, respectively. The important phases of development period during

entire life cycle of all rice and wheat cultivars have been given in Fig. A 1 & 2. The reproductive stage of all the cultivars was divided into five stages, such as anthesis (0 day after anthesis or 0 DAA), grain-filling (0-7 days after anthesis or 7 DAA), grain development (7-14 days after anthesis or 14 DAA), grain maturation (14-21 days after anthesis or 21 DAA) and senescent stages (21-28 days after anthesis or 28 DAA).

2.2.2. Cultivation of plants :

Certified and healthy seeds of above mentioned rice cultivars were collected from the Crop Research Farm of Burdwan University and Rice Research Institute, Chinsurah, West Bengal, and wheat cultivars were procured from Agricultural University, Pantnagar, U.P., India. Seeds were surface sterilized in 0.1% (w/v) mercuric chloride (HgCl_2) for one minute and washed thoroughly several times in sterile distilled water. Seeds were then germinated in plastic trays containing moistened blotting paper at 37°C in a germinator. The germinated seeds of rice were sown in the seed-bed and 30-day-old seedlings were then transplanted in the field in 5 m^2 plots, with one seedling per hill at the spacing of 25 x 25 cm distance between plants. On the other hand, germinated seeds of wheat were directly sown in the field in 5 m^2 plots, in different rows at a distance of 45 cm between the rows and 15 cm between plants.

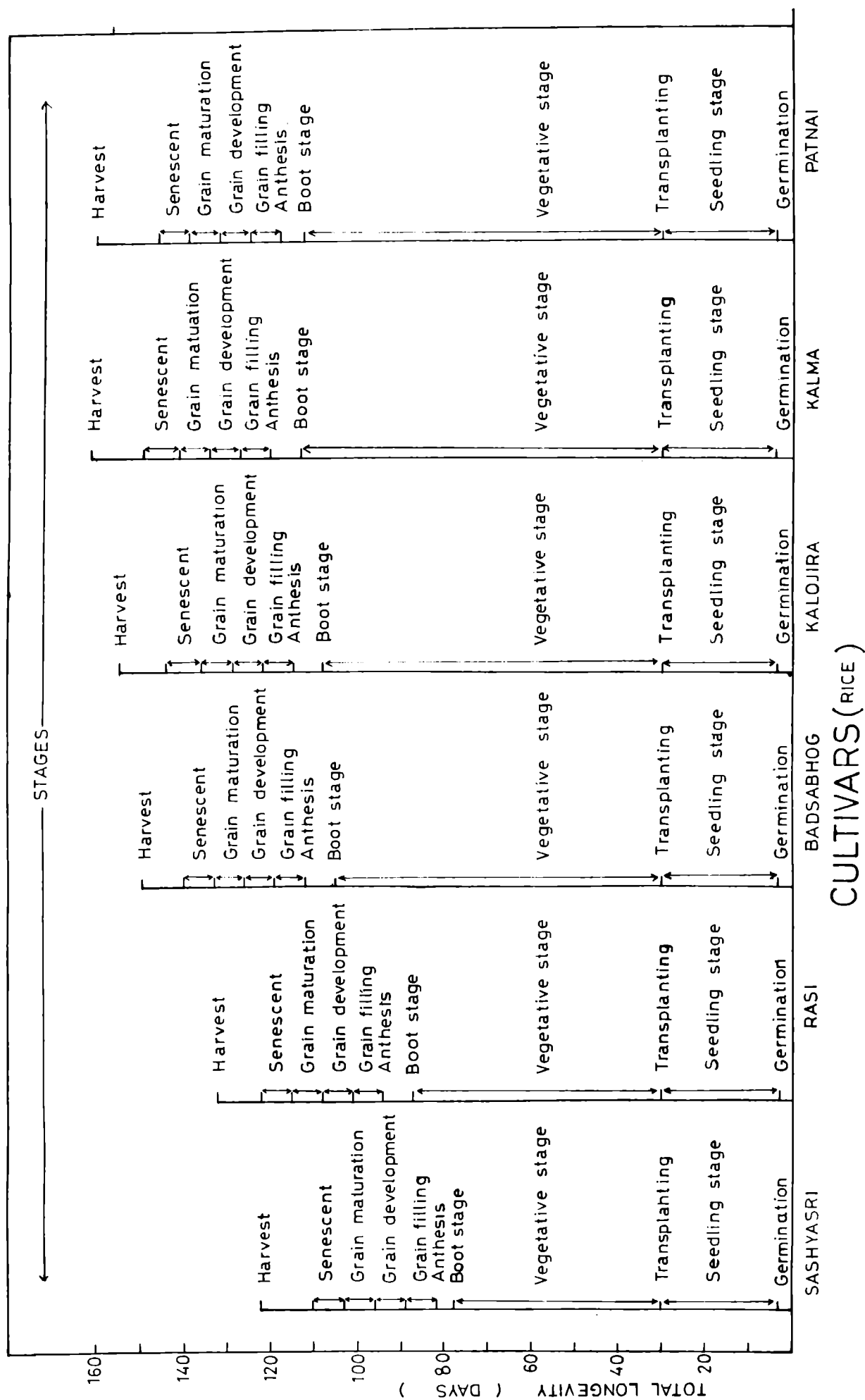


Fig. AI - Developmental stages of six rice cultivars.

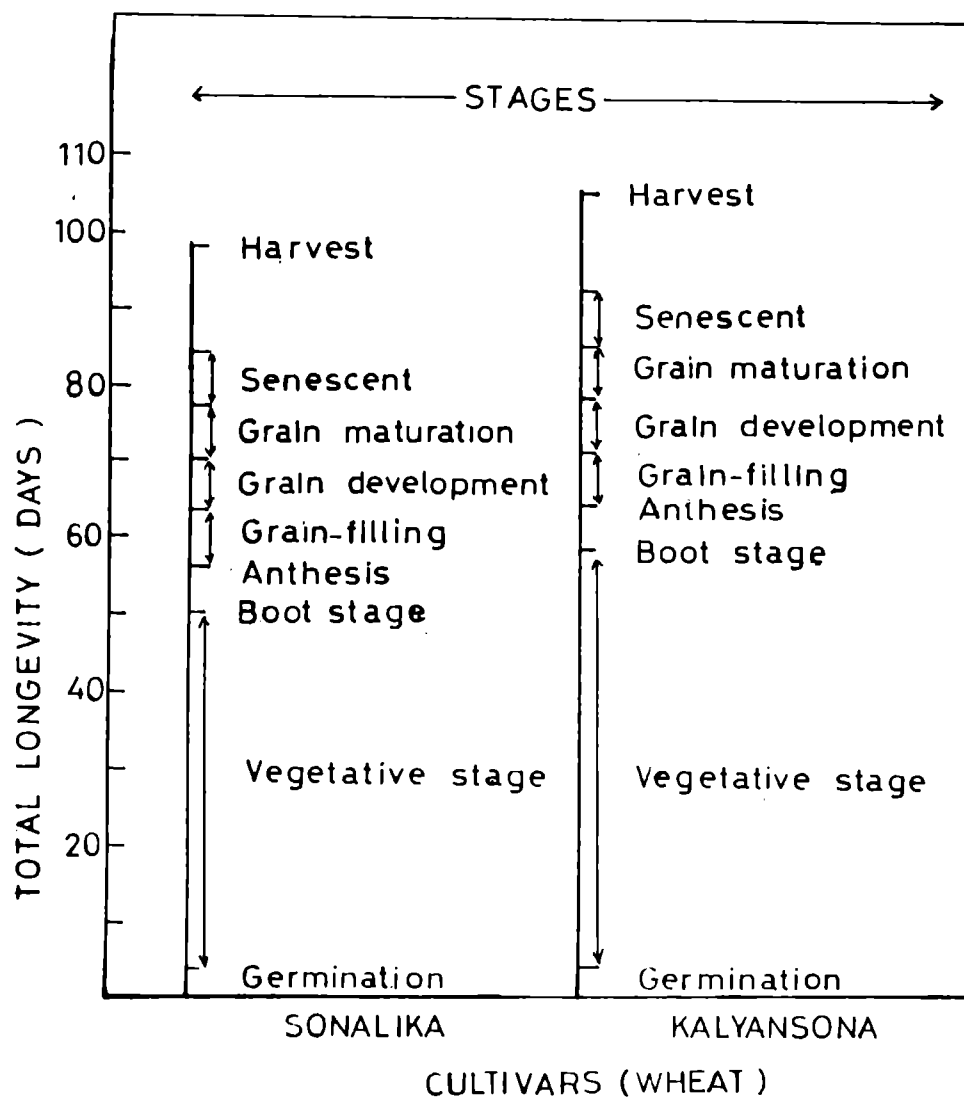


Fig. AII - Developmental stages of two wheat cultivars.

Before cultivation the soil was prepared by mixing cowdung as the only manure at the rate of 2 Kg/m² land for both the plants and watering was done at regular intervals.

2.2.3. Soil composition :

The average NPK composition of the soil of the cultivated land was as follows : nitrogen 0.20%, phosphorus (as P₂O₅) 0.047%, potassium 0.016% . The pH of the soil was around 6.4.

2.2.4. Design of experiments :

The following experiments were done to analyse the patterns of leaf senescence and to elucidate the possible mechanisms of monocarpic senescence in rice and wheat plants. The experimental designs are described below.

2.2.4.1. Study of leaf senescence behaviour of rice and wheat cultivars at the reproductive stage :

To study the leaf senescence behaviour of the flag, second and third leaf of six rice cultivars (viz., Rasi, Sashyasri, Kalojira, Badsabhog, Patnai and Kalma) and two wheat cultivars (viz., Sonalika and Kalyansona), the changes in chlorophyll and protein contents were measured at intervals of 7 days starting from anthesis (0 DAA) up to the senescent stage (28 DAA). In most of the senescence experiments reported here, decline in chlorophyll and protein was taken as indicator of leaf senescence (32).

The leaf senescence patterns were also studied by considering total leaf area and percentage of yellow patches of total leaf area. The changes in nitrogen and phosphorus contents were also measured in the flag, second and third leaf of Rasi, Kalojira and Patnai rice and Sonalika wheat cultivars at intervals of 7 days during reproductive development. To elucidate the relationship with sink strength and nutrient mobilization, the total panicle weight was measured in different rice and wheat cultivars.

2.2.4.1.2. Assessment of [^{32}P]-phosphate retention and mobilization from the leaves to grains of three rice and one wheat cultivars :

To study the role of nutrient mobilization in leaf senescence behaviour, the pattern of retention and mobilization of [^{32}P]-phosphate from the flag, second and third leaf to the grains was studied at intervals of 7 days, starting from anthesis (0 DAA) upto the senescent stage (28 DAA), during reproductive development of three rice (viz. Rasi, Kalojira and Patnai) and one wheat (Sonalika) cultivars.

2.2.4.1.3. Assessment of [^{32}P]-phosphate mobilization patterns from roots to the flag, second and third leaf and grains during reproductive development of rice and wheat cultivars :

To elucidate the role of xylem flux containing nutrients and hormones from the roots to the vegetative and reproductive

parts in leaf senescence behaviour, the mobilization patterns of [^{32}P]-phosphate from roots to the flag, second and third leaf and to the grains was analysed at intervals of 7 days, starting from anthesis (0 DAA) up to the senescent stage (28 DAA), during reproductive development of the above-mentioned three rice and one wheat cultivars.

2.2.4.1.4. Study of correlation of senescence patterns with xylem parameters at the juncture of leaf lamina and leaf sheath :

To study the correlation of senescence pattern with the xylem parameters the number of vascular bundles at the juncture of leaf lamina and leaf sheath, area of vessels in a bundle and the area of the lumen of largest vessel were recorded in three rice and one wheat cultivars.

2.2.4.2. Effects of hormones on the patterns of leaf senescence in rice and wheat cultivars during reproductive development :

The role of hormones on the regulation of monocarpic senescence and their effects on modification of leaf senescence behaviour were observed in two rice (Rasi and Kalojira) and one wheat cultivars (Sonalika). Rice and wheat cultivars were grown in the field and divided into 5 blocks for each cultivar. Four such blocks were used for treatments and the remaining one served as control. Benzyladenine (BA, 4.4×10^{-4} M), gibberellic acid (GA_3 , 2.9×10^{-4} M), abscisic acid

(ABA, 7.5×10^{-5} M) and a combination of (BA + GA₃) (4.4×10^{-4} M and 2.9×10^{-4} M) were separately sprayed foliarly at intervals of 7 days on the rice and wheat cultivars in their stipulated blocks during their reproductive development, starting from the anthesis stage.

2.2.4.2.1. Effects of hormones on chlorophyll and protein contents in the leaves during the progress of reproductive development of rice and wheat cultivars :

Effects of the above hormones were studied on the modification of leaf senescence behaviour in terms of decline in chlorophyll and protein level in the flag, second and third leaf during reproductive development of rice and wheat cultivars at intervals of 7 days starting from the grain-filling (7 DAA) to the senescent stage (28 DAA).

2.2.4.2.2. Effectsof hormones on nitrogen and phosphorus contents in the leaves during the progress of reproductive development of rice and wheat cultivars:

Effects of above hormones on the changes in nitrogen and phosphorus contents in the flag, second and third leaf of the above mentioned rice and wheat cultivars were studied at intervals of 7 days during their reproductive development, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

2.2.4.2.3. Effects of BA and ABA on retention and mobilization of [32 P]-phosphate from different leaves to the seeds during reproductive development of rice and wheat cultivars :

The retention capacity of [32 P]-phosphate in the flag, second and third leaf and mobilization from each leaf to the developing seeds were recorded at intervals of 7 days in untreated control and treated rice and wheat cultivars during their reproductive development, starting from the grain-filling (7 DAA) to the senescent stage (28 DAA).

2.2.4.3. Certain biochemical and enzymatical changes associated with leaf senescence during reproductive development of rice and wheat cultivars and effects of hormones on them:

Rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) plants were cultivated in the field and divided into 3 separate blocks for each cultivar and BA and ABA were foliarly sprayed in the respective blocks of each cultivar as described in the experiment 2.2.4.2. The changes in RNA, histone protein, total free amino acids and malondialdehyde contents and activities of a few enzymes generally associated with cellular degradation and free radical metabolism (viz. protease, catalase, peroxidase and superoxide dismutase) were observed at intervals of 7 days in the control and treated rice and wheat cultivars during their reproductive development, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

2.2.4.4. Changes in the transpiration rate and proline accumulation during reproductive development of rice and wheat cultivars and effects of hormones (BA and ABA) on them :

It is well known that hormones regulate senescence by stomatal movement which further affects the distribution of nutrients and hormones from the roots to the aerial parts. Again, stress-induced proline accumulation affects stomatal movement. Thus, in the present study the rate of transpiration and proline accumulation and effects of benzyladenine (BA) and abscisic acid (ABA) on them were studied in rice and wheat cultivars.

Rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) plants were grown in the field and divided into 3 blocks for each cultivar. Two such blocks were used for treatments and the remaining one served as control. BA (4.4×10^{-4} M) and ABA (7.5×10^{-5} M) were separately sprayed foliarly as done in the previous experiment. The changes in the rate of transpiration by the whole plant (main tiller) and by each leaf (flag, second, third) and proline accumulation in the flag, second and third leaf were recorded at intervals of 7 days during the reproductive development of above mentioned control and treated rice and wheat cultivars, starting from the grain-filling up to the senescent stage. The leaves were smeared with vaseline on both sides except the desired leaf and the rate of transpiration from this leaf was calculated.

2.2.4.5. Changes in the endogenous level of cytokinin-like substances (CK), abscisic acid and ethylene in the leaves of rice and wheat cultivars during reproductive development :

Changes in the endogenous level of CK-like substances, abscisic acid and ethylene evolution were recorded in the flag, second and third leaf, at intervals of 7 days during the reproductive development of rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) plants, starting from the anthesis (0 DAA) up to the senescent stage (28 DAA).

2.2.4.6. Changes in the protein, nucleic acids (RNA, DNA) and histone protein contents in the shoot apex during transition from vegetative to reproductive stage of rice and wheat cultivars :

To partially assess changes in the genetic materials such as histone protein, nucleic acids and total protein in the shoot apex (which is subsequently transformed into reproductive axis) these components were analysed in the shoot apex. The shoot apices were collected from the different aged rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) cultivars 18-24 days before panicle emergence, at intervals of 2 days till the advent of panicle emergence. Collections of shoot apices were made at the plant age starting from 71 and 94 days up to 86 and 106 days for Rasi and Kalojira rice cultivars, respectively, and from 38 days up to 53 days for Sonalika wheat cultivar.

2.2.4.7. Experiments with surgically altered rice and wheat cultivars :

Analyses of the mechanism of monocarpic senescence and the correlative control and effects of one organ on the other was done by surgical treatments of the plants. Thus, different surgically manipulative experiments were carried out on rice and wheat cultivars to elucidate the mechanism of monocarpic senescence. The surgical experiments undertaken for this purpose are described below.

2.2.4.7.1. Effect of panicle removal at different stages of reproductive development of rice and wheat cultivars:

The experiment was performed to analyse the role played by the leaves on whole plant senescence through mobilization of metabolites and which stage of reproductive development is most susceptible for initiating senescence. The role of panicles at different reproductive stages on senescence was also studied.

The rice and wheat cultivars grown in the field were divided into 5 blocks for each cultivar. The panicles were excised at the anthesis stage (0 DAA), grain-filling stage (7 DAA), grain-development stage (14 DAA) and grain maturation stage (21 DAA) from the respective blocks of both rice and wheat cultivars. The remaining block with plants containing intact panicles served as control. The following changes in control and surgically treated cultivars were observed.

2.2.4.7.1.1. Study of leaf senescence behaviour of the flag, second and third leaf of control and surgically treated rice and wheat cultivars :

The leaf senescence behaviour of the control and treated rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) cultivars from which the panicle was removed was observed in terms of decline in chlorophyll and protein contents in the flag, second and third leaf throughout the reproductive development, starting from the anthesis (0 DAA) up to the senescent stage (28 DAA).

2.2.4.7.1.2. Study of glume senescence in rice and wheat cultivars :

It was observed in the above experiments that the delaying effect of the removal of panicle on the leaf senescence was significantly less pronounced in wheat than in rice cultivars. So, it was thought worthwhile to study the senescence behaviour of the glumes which are secondary source of photosynthate in cereals. This study might reveal the relative contribution of photosynthate by the reproductive structures associated with photosynthesis. Hence, the decline in chlorophyll and protein in the glumes of intact rice and wheat cultivars during reproductive development was studied.

2.2.4.7.1.3. Changes in nitrogen and phosphorus contents in the leaves of control and surgically treated rice and wheat cultivars :

Effect of panicle removal at different reproductive stages (0, 7, 14 and 21 DAA) on changes in nitrogen and phosphorus contents in the flag, second and third leaf were observed and recorded in both rice and wheat cultivars during their reproductive development, at intervals of 7 days, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

2.2.4.7.1.4. Assessment of [^{32}P]-phosphate retention capacity of each fed-leaf and of the stem (when fed through flag leaf only) of control and treated rice and wheat cultivars :

The effect of panicle removal on [^{32}P]-phosphate retention capacity of the fed flag, second and third leaf and of the stem (when fed through flag leaf only) were observed in the control and treated rice and wheat cultivars during their reproductive development, at intervals of 7 days, starting from the grain-filling stage (7 DAA) up to the senescent stage (28 DAA).

2.2.4.7.2. Effects of defoliation of a leaf (flag, second and third separately) on the senescence of remaining leaves of rice and wheat cultivars :

To study the role played by each leaf on grain development, which could also modify the senescence process of the remaining

leaves, and to elucidate the cause of monocarpic senescence, the following experiment was carried out. A particular leaf from the top was removed and its effect on the senescence of the remaining leaves was studied. The rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) cultivars were grown in the field and divided into 4 blocks as described earlier. From such blocks, the flag, second or third leaf was separately removed at the anthesis stage. The fourth block having intact plants served as control.

2.2.4.7.2.1. Studies on the leaf senescence behaviour of control and remaining leaves of surgically treated plants of rice and wheat cultivars :

Leaf senescence behaviour of the flag, second and third leaf of control and remaining leaves of the surgically treated rice and wheat plants was noted in terms of decline in chlorophyll and protein contents during reproductive development, at intervals of 7 days, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

2.2.4.7.2.2. Changes in nitrogen and phosphorus contents in the leaves of control and treated rice and wheat cultivars :

Effect of leaf removal at the anthesis stage on changes in nitrogen and phosphorus contents of the remaining attached leaves of the surgically treated plants over the flag, second and third leaf of control plants of rice and wheat cultivars

were observed and recorded at intervals of 7 days during their progress of reproductive development.

2.2.4.7.2.3. Effects of defoliation on mobilization of [^{32}P]-phosphate from the remaining leaves to grains during reproductive development of rice and wheat cultivars :

To study the role played by the three uppermost leaves in mobilization of nutrients and its influence on the whole plant senescence, the mobilization pattern of [^{32}P]-phosphate from the flag, second and third leaf of control plants and from the remaining leaves of surgically treated plants to the grains was observed and recorded at intervals of 7 days during reproductive development of rice and wheat cultivars, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

2.2.4.7.3. Effects of removal of different percentage of spikelet or emasculation on whole plant senescence of rice and wheat cultivars :

To study the source-sink relationship and its influence on the whole plant senescence, this experiment was carried out where 25, 50, 75 and 100 percent of the spikelets were removed manually from the panicle or emasculated by hot water treatment (55°C for 5 minutes) at the anthesis stage during reproductive development of both rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) cultivars. Intact rice and wheat

plants served as control. The development of secondary branches at the axil of second leaf of the main tiller was recorded. When the secondary branches developed and attained the anthesis stage, they were also subjected to above surgical treatments in an identical way which led to the development of tertiary branch at the second leaf axil of secondary branch in a few cases of such treatments in the two rice cultivars and these were recorded. When such treatment was repeated in the tertiary branch, no further (i.e., quaternary) branch developed.

The seed production capacity and leaf area of the flag and second leaf of the main tiller, the secondary and tertiary branches of rice and only of the main tiller of wheat cultivar (where side branch development did not occur) were recorded.

2.2.4.7.3.1. Study of leaf senescence behaviour of control and treated main tiller, secondary and tertiary branches of rice cultivars and the main tiller of wheat cultivar :

The leaf senescence behaviour was observed in terms of decline in chlorophyll and protein contents of the top three leaves of control and surgically treated main tillers of rice and wheat cultivars and the two topmost leaves of the secondary and tertiary branches of rice cultivars (control and treated) during their reproductive development. Chlorophyll and protein contents were measured at intervals of 7 days during their reproductive development, each branch taken separately.

2.2.5. Methods

2.2.5.1. Measurement of leaf area and xylem parameters :

The area of the flag, second and third leaf of the experimental plants was measured by simple graphical method and expressed as cm^2 .

The number of vascular bundles was observed under a compound microscope in hand-made cross sections. The area of xylem vessels and that of lumen of the largest vessel were also recorded under a compound microscope after standardization of the ocular with the help of a stage micrometer and the data were expressed as μm^2 .

2.2.5.2. Methods of feeding of [^{32}P]-phosphate through leaves and assessment of its retention and translocation to different parts :

In all experiments, 1 ml of ^{32}P as $\text{H}_3^{32}\text{PO}_4$ (19.19 MBq) in 0.1 M sodium citrate buffer (pH 6.5) was fed separately through the tip of flag, second and third leaf by ~~deeping~~^{dipping} 1 cm of the tip portion into a vial containing isotope solution for 24 h. After feeding, randomized samples were collected from the individual organ (flag, second, third leaf and grains, as well as stem and branches as desired) and dried separately on planchettes under an infra-red lamp (Philips, India) for 24 h. After

proper drying the radioactivity of the fed leaves and that of the grains (or other parts if necessary) were measured in a Geiger-Muller counting system (Model No. ECIL-GCS M-A, India). The retention and mobilization of [^{32}P]-phosphate were expressed as $\text{KBq. leaf}^{-1} \text{ h}^{-1}$.

2.2.5.3. Methods of feeding of [^{32}P]-phosphate through roots and assessment of translocation to different leaves and grains :

After careful washing, the total roots of rice and wheat plants of each cultivar, the ^{32}P as $\text{H}_3^{32}\text{PO}_4$ (19.19 MBq) in 0.1 M sodium citrate buffer (pH 6.5) was fed for 5 h by deeping the roots into 10 ml isotope solution. The randomized samples were collected separately from the flag, second and third leaf and grains. The samples were then dried on planchettes under infra-red lamp for 24 h. The radioactivity of the samples^{was} measured in a Geiger-Muller counting system. The mobilized [^{32}P]-phosphate was expressed as $\text{KBq leaf}^{-1} \text{ h}^{-1}$.

2.2.5.4. Method of foliar spraying of hormones :

Aqueous solutions of benzyladenine (BA), abscisic acid (ABA), gibberellic acid (GA_3), and a combination of (BA + GA_3) were adjusted to pH 7 with 0.1(N) NaOH and foliarly sprayed at intervals of 7 days using 0.5% Teepol as a surfactant at the rate of 5 ml/plant in the respective block of rice and wheat cultivars during their reproductive development starting

from the anthesis (0 DAA) up to the senescent stage (28 DAA). Spraying was done with the help of a hand sprayer in the morning to avoid scorching. Control plants were also sprayed with an aqueous 0.5% Teepol solution only.

2.2.6. Method of estimation of biomolecules, enzymes and hormones :

2.2.6.1. Chlorophyll :

The chlorophyll content of leaf tissues was measured following the method of Arnon (11). Fifty milligram leaf tissues were homogenized in 5 ml cold methanol and centrifuged at 6000 rpm for 10 min and the supernatant was collected. The pellets were subsequently washed in methanol and centrifuged again. Then the absorbance of the combined supernatant was measured at 650 nm in a Spectrochem spectrophotometer (AIMIL, Calcutta, Model No.RT-135). The chlorophyll content was determined and expressed as mg.g^{-1} fresh weight (FW).

2.2.6.2. Protein :

For protein estimation, chlorophyll-free leaf samples were homogenized with 80% ethanol and centrifuged at 6000 rpm for 10 min. The pellets were then made phenol-free by washing successively with 10% (w/v) trichloroacetic acid (TCA), ethanol, ethanol : chloroform (3:1), ethanol:ether (3:1) and finally with ether according to Kar and Mishra (179).

The pellets were dried and solubilized by treating with 2 ml 1.0(N) NaOH at 80°C for an hour in water-bath. After proper dilution, the protein content was measured following the method of Lowry et al (216), by reacting with Folin-phenol reagent. One ml of diluted extract was mixed with 1 ml of solution A (10% Na₂CO₃ in 0.05 (N) NaOH : CuSO₄.5H₂O:Na-K tartrate = 20:1:1) and allowed to stand for 10 min. Then 3 ml of working Folin reagent were added to it rapidly. The solution was kept for about 30 min and the OD value was measured at 650 nm in a Spectrochem spectrophotometer. The actual protein content of the leaf samples was determined by comparing the OD value of the standard curve prepared from bovine serum albumin (BSA, Fraction V powder, Sigma Chemical Co.,USA) and expressed as mg.g⁻¹ fresh weight.

2.2.6.3. Nucleic acids :

Nucleic acids (DNA and RNA) were extracted from the samples following the method of Cherry (57). RNA was estimated according to Markham (233) by orcinol reagent as modified by Choudhuri and Chatterjee (62). Three ml of the extracted solution (diluted) was mixed with 3 ml of orcinol reagent (1 g orcinol in 100 ml conc. HCl (AR) containing 0.1% FeCl₃.6H₂O). After proper mixing the solution was heated in water-bath at 100°C for 20 min with glass marble at the top of each test tube to prevent splashing. The solutions were then cooled at room temperature and the

intensity of green colour was measured at 700 nm in a Spectrochem spectrophotometer. Also the intensity of blank set was measured containing 3 ml distilled water instead of plant extract and the sample reading was corrected. The actual RNA content was calculated by comparing the OD value of the standard curve prepared from yeast RNA (Type II, Biochemical Unit, V.P. Chest Institute, India) and the value was expressed as mg.g^{-1} fresh weight.

The DNA content of the samples was measured by following the method of Burton (49). One ml of extracted DNA was mixed with 5 ml diphenylamine reagent (1 gm of diphenylamine in 100 ml glacial acetic acid (AR, BDH), containing 2.75 ml concentrated AR H_2SO_4). The solution was then heated in a waterbath for 1 h at 100°C with glass marble at the top of each test tube. After heating, the solution was cooled to room temperature and the intensity of blue colour developed was measured at 600 nm in a Spectrochem spectrophotometer deducting the blank reading done in an identical manner, but with H_2O instead of sample. DNA content was calculated by comparing the OD value of the standard curve prepared from herring sperm DNA (Sigma Chemical Co.) and expressed as ng.g^{-1} fresh weight.

2.2.6.4. Histone protein :

Histone protein was extracted following the method of Gornall et al.(129). Leaf samples (1 gm) were homogenized

in cold 8 ml 0.3(N) HCl. The extract was centrifuged at 8000 rpm for 10 min. The residue was again extracted. After centrifugation the supernatant was mixed with solid TCA to a final concentration of 20% for precipitation of protein fraction. The precipitation was then washed with acetone containing 1.0% HCl and followed by pure acetone only and air-dried. Finally, the precipitate was dissolved in a fixed volume of distilled water and the histone protein content was measured by Folin-phenol reagent according to the method already described and expressed as $\text{mg}\cdot\text{g}^{-1}$ fresh weight.

2.2.6.5. Free amino acid :

The extraction of free amino acids was done following the method of Dwivedi et al. (93). The leaf samples (100 mg) were homogenized with 8 ml 80% ethanol and kept for 15 min at 60°C. The solution was then centrifuged at 6000 rpm for 10 min. The supernatant was taken in glass Petridishes and dried on a hot plate. The chlorophyll was then removed by rinsing thrice with 5 ml ether. To this 5 ml of 80% ethanol were then added to the Petridish and stirred well. The extract was then used for the estimation of total free amino acids following the method of Moore and Stein (262). One ml of the extract was mixed with 3 ml of 0.1% ninhydrin solution (in 80% ethanol) in a test tube and heated in a waterbath at 100°C for 15 min with a glass marble at the top to avoid splashing. The solution was then cooled to room temperature and the volume was

adjusted to 4 ml. The intensity of the purple colour developed was measured at 480 nm in a Spectrochem spectrophotometer. The quantity of total free amino acids was measured by comparing with the OD value of a standard curve prepared from glycine (Sigma Chemical Co.) and expressed as mg.g^{-1} fresh weight.

2.2.6.6. Proline :

The proline content of the leaf samples was measured according to Bates et al.(19). Leaf samples were homogenized with 6 ml of 3% sulfosalicylic acid and centrifuged at 6000 rpm for 10 min. Two ml of the extract were then mixed with 2 ml of acid ninhydrin solution (1.25 gm ninhydrin in 30 ml glacial acetic acid + 20 ml of 6 M orthophosphoric acid + 5 ml distilled water). The mixture was heated in a water-bath at 100°C for 1 h. After heating, the mixture was kept overnight inside the ice-chamber. The proline was separated from the mixture by 4 ml of toluene with the help of a separating funnel. The intensity of yellow-orange colour was measured at 520 nm in a Spectrochem spectrophotometer. The actual value of proline was estimated by comparing with the OD value of a standard curve prepared from proline (Sigma Chemical Co.) and expressed as ng.g^{-1} fresh weight.

2.2.6.7. Nitrogen :

Nitrogen content of the leaf samples was measured following the method of Vogel (428). Dried leaf samples were

digested in 2 ml of conc. H_2SO_4 (AR) for 1 h. After digestion, a few drops of hydrogen peroxide (H_2O_2) were added and heated until the colour of the solution disappeared. The volume of the sample was made up to 50 ml by adding distilled water. One ml of this extract was mixed with 1 ml of a mixture of 10% sodium hydroxide and 10% sodium silicate (1:1) and finally with 5 ml of Nessler's reagent (K_2HgI_4). After 15 min the intensity of yellow colour was measured at 410 nm in a Spectrochem spectrophotometer. Similarly, a blank set was made containing 1 ml of distilled water instead of extract. The nitrogen content was determined by comparing with the OD value of a standard curve prepared with $(\text{NH}_4)_2\text{SO}_4$ and expressed as mg.g^{-1} dry weight.

2.2.6.8. Phosphorus :

The ash obtained from 1 gm dried leaf samples was dissolved in 2 ml of conc. H_2SO_4 (AR). Then the solution was diluted up to 100 ml and filtered through a Whatman No.1 filter paper. Three ml of the filtrate were mixed with 1 ml of freshly prepared chromogenic reagent for inorganic phosphorus determination following the method of Jaffe and Galston (1966). The mixture was then incubated for 15 min at 30°C and the intensity of the blue colour developed after reaction was measured immediately at 650 nm in a Spectrochem spectrophotometer. A blank was similarly prepared by adding 3 ml of distilled water instead of extract. The value of phosphorus

was determined from a standard curve prepared by $\text{Na}_3\text{PO}_4 \cdot 12\text{H}_2\text{O}$ (AR) and the phosphorus content was expressed as mg.g^{-1} dry weight.

2.2.6.9. Measurement of malondialdehyde (index of membrane lipid peroxidation) :

Malondialdehyde is a decomposition product of the oxidation of polyunsaturated fatty acids of the biomembrane. This was estimated following the method of Heath and Packer (148). Five hundred mg leaf samples were homogenized in 5 ml of 1% TCA and then centrifuged at 10,000 rpm for 10 min. One ml of the supernatant was mixed with 3 ml of 5% TCA containing 1% thiobarbituric acid (TBA, Sigma Chemical Co.). The mixture was then heated in a boiling water-bath for about 30 min and then quickly cooled in an ice-bath. The solution was centrifuged at 10,000 rpm for 10 min and the absorbance was read at 530 nm in a Spectrochem spectrophotometer. The unspecific turbidity was corrected by subtracting A_{600} from A_{530} . The quantity of malondialdehyde was measured from its extinction coefficient of $155 \text{ m M}^{-1} \text{ cm}^{-1}$ (148).

2.2.6.10. Extraction and assay of enzymes :

2.2.6.10.1. Catalase (EC 1.11.1.6) :

Catalase activity was measured according to the method of Chance and Maehly (54) as described by Snell and Snell (387). The enzyme was extracted from 200 mg leaf samples by

homogenizing with 6 ml of 0.1 M Na-phosphate buffer (pH 6.8) in an ice-cold condition. The homogenate was centrifuged at 10,000 rpm for 10 min in a cold centrifuge (0°C). The supernatant was used as an enzyme source.

The activity was measured by reacting 1 ml of extract with 2 ml of 0.0025 M H_2O_2 for 10 min at 37°C in an incubator. The reaction was stopped by adding 1 ml of 1% Titanic sulphate in 25% H_2SO_4 (v/v) and the mixture was centrifuged at 6000 rpm for 15 min. The intensity of yellow colour was measured at 410 nm in a Spectrochem spectrophotometer.

2.2.6.10.2. Peroxidase (EC 1.11.1.7) :

Two hundred mg leaf samples were homogenized with 10 ml of 0.1 M Na-phosphate buffer (pH 6.8) in an ice-cold condition and centrifuged in cold condition at 17,000 rpm for 15 min. The supernatant was then used as an enzyme source.

The enzyme activity was measured following the method of Kar and Mishra (179). One ml of diluted enzyme extract was mixed with the following solutions : 1.5 ml of 125 μmole phosphate buffer (pH 6.8), 1 ml 15 μmole pyrogallol, 1 ml 50 μmole H_2O_2 and 0.5 ml distilled water. The reaction mixture was then incubated for 15 min at 25°C. After incubation the reaction was stopped by adding 0.5 ml of 5% H_2SO_4 . The amount of purpurogallin formed was determined by measuring the absorbance at 420 nm in a Spectrochem spectrophotometer. A blank set was similarly prepared where 1 ml distilled water was added instead of enzyme source.

2.2.6.10.3. Superoxide dismutase (SOD, EC 1.15.1.1) :

The enzyme was extracted by homogenizing 500 mg leaf samples in 5 ml 0.1 M K-phosphate buffer (pH 7.8) containing 1% (w/v) ethylene diamine tetraacetic acid (EDTA) in an ice cold condition. The homogenate was centrifuged successively at 5000 and 13,000 rpm at 0°C for 15 min and 20 min, respectively. The supernatant was used as crude enzyme source.

The reaction mixture for this enzyme activity consists of 1 ml Na_2CO_3 (0.05 M), 0.5 ml 15 μ M methionine, 0.5 ml 0.1 μ M EDTA, 0.1 ml of 63 μ M nitroblue tetrazolium (NBT), 2 ml enzyme extract and 0.5 ml 1.5 μ M riboflavin. Then the mixture was incubated under white fluorescent lamp (HMT, 40 W) at the intensity 180 μ mole. m^{-2} sec^{-1} at 30°C for 30 min. After incubation the reaction was stopped by adding 1 ml of 0.2 M potassium cyanide (KCN). Also, a blank was prepared by adding 1 ml of KCN before incubation. The intensity of colour was recorded at 560 nm in a Spectrochem spectrophotometer.

The activity was determined by measuring its ability to inhibit photochemical reduction of NBT according to the method of Giannopolitis and Ries (124) with slight modifications (350). The reduction of NBT is inversely proportional to the enzyme activity. Thus to obtain ΔA , A_{560} of the particular set was deducted from A_{560} of the blank set, i.e., where the enzyme was killed before incubation.

2.2.6.10.4. Protease (EC 3.4.4X) :

Protease activity was measured according to the method of Snell and Snell (387) as modified by Biswas and Choudhuri (30). The enzyme was extracted by homogenizing 1 gm of leaf tissue in 10 ml of 0.1 M Na-phosphate buffer (pH 6.5) in an ice-cold condition. The homogenate was then centrifuged at 10,000 rpm at 0°C for 15 min and the supernatant was used as crude enzyme source.

The reaction mixture for measuring protease activity consists of: 1 ml enzyme extract, 0.1 ml of 0.1 M MgSO_4 and 1 ml bovine serum albumin (BSA, 50 $\mu\text{g/ml}$). The reaction mixture was incubated at 37°C for an hour and then the reaction was stopped by adding 1 ml 25% TCA. A blank set was prepared where enzyme was killed before incubation by heating. The residual protein was measured by Folin-phenol reagent according to Lowry et al. (2161).

If not mentioned otherwise, in each case of enzyme assay, the zero time control was taken as blank and the activity of each enzyme was expressed as $[\Delta A \times T_v / (t \times v)]$, where, ΔA is the absorbance of the sample after incubation minus the absorbance at zero time control, T_v is the total volume of enzyme extract, t is the time (min) of incubation and v is the volume of extract taken for assay (103). The enzyme activity was expressed as enzyme unit $\text{min}^{-1} \text{g}^{-1}$ fresh weight.

2.2.6.11. Transpiration :

The root systems of the main tiller of rice and wheat cultivars after proper washing, were introduced into a specially designed 250 ml flask (wide mouth) which was filled with water. The 2 ml oil was poured into the surface of water to check the evaporation of surface water. The total set up was weighed and allowed to stand in the laboratory under the light intensity of $200 \mu \text{mole.m}^{-2} \text{sec}^{-1}$ at $25 \pm 2^\circ\text{C}$. After three hours, the total set-up was reweighed. The difference between the first and the second weight gave the amount of water transpired by the plant (63). The total leaf area was measured by simple graphical method. The rate of transpiration was expressed as $\text{mg H}_2\text{O cm}^{-2} \text{h}^{-1}$. In another experiment, the transpiration rate of a single leaf was measured by smearing both surfaces of the remaining leaves with vaseline.

2.2.6.12. Extraction, identification, purification and estimation of abscisic acid, cytokinin-like substances and ethylene :

2.2.6.12.1. Abscissic acid (ABA) :

Extraction and fractionation of ABA were done according to Wright (457). Leaf samples (80 g) were homogenized with 80% methanol (10 ml/g) and extracted at 5°C for 24 hours. The procedure was repeated once again. Methanol was evaporated in vacuo at 40°C . The residue was reconstituted in

40 ml of warm distilled water (35°C) and the aqueous extract was adjusted to pH 2.5 with 0.1 N HCl and the free ABA was extracted three times with diethylether (peroxide free). Anhydrous sodium sulphate was mixed with total ether layer and kept for 2-3 hours for drying of aqueous layer. The ether layer containing free ABA-like substances was dried. The residue was then redissolved in a small volume of 80% methanol and stored at 2°C until used. The layer which was partitioned against the ether layer was then taken for the determination of bound ABA. The pH was adjusted to 7.0 with dilute NaOH [0.01(N)] stored at 2°C overnight, pH was again adjusted to 11.0 with dilute NaOH and warmed at 65°C for 24 hours. After hydrolysis, the solution was rapidly cooled, pH was adjusted to 2.5 with dilute HCl [0.01(N)].

Fractionation was done in the manner described for free ABA. The residue was dissolved in a small volume of methanol and stored at 2°C. All the above extracts were further purified on silica gel coated TLC plates.

Purification of ABA : An aliquot of the extract containing ABA was spotted with the help of a capillary tube on the activated TLC plates (30 min at 100°C). After spotting, the plates were developed in a mixture of isopropanol:ammonia:water (10:1:1) and the zone on the plates corresponding to ABA marker spot (i.e. UV fluorescent spot of authentic ABA) was scraped off and eluted with methanol and stored at 20°C for

48 hours. The solution was again purified on TLC plate in the same manner. The extracted ABA was then used for gas chromatography.

Estimation of ABA by gas chromatography (GC) : The authentic ABA (as standard) and TLC purified ABA extracts were methylated by diazomethane and used for GC.

Preparation of diazomethane and methylation of samples : Diazomethane was prepared following the method of Vogel (427) as follows :

Part-A : Preparation of acetyl-methyl urea : A solution of 17.7 g of acetamide (CH_3CONH_2) in 9 ml liquid bromine was taken in a beaker and 12 g of sodium hydroxide (NaOH) in 48 ml distilled water was added dropwise with hand stirring placing the beaker on a steam bath for dissolution of acetamide. But care was taken to minimize the loss of bromine due to heating.

The resulting mixture (yellow in colour) was heated on the steam bath until effervescence set in. The heating was permitted for additional 3 min. Crystallization of acetyl-methyl urea was obtained from the yellow to red colour solution. The crystallization was completed by cooling the reaction mixture in an ice-bath for an hour. Finally, the acetyl-methyl urea was obtained by filtration and air-drying.

Part-B : Preparation of nitrosomethyl urea : A mixture of 12 g of acetylmethyl urea and 12 ml concentrated HCl (AR) were heated with hand stirring until the solid acetylmethyl urea was dissolved. Heating was continued for an additional 2-3 min. And the resulting solution was diluted with an equal volume of distilled water and cooled below 0°C in an ice-bath. A cold sodium nitrite solution (38 g in 55 ml water) was added to the above solution slowly with stirring. The reaction was completed on an ice-bath for several minutes for precipitation. The precipitate of N-nitro-N-nitroso-methyl urea was filtered and washed with 8-10 ml of ice cold distilled water.

Part-C : Formation of diazomethane : In an Erlenmeyer's flask, 3 ml of 50% potassium hydroxide (KOH) and 10 ml diethyl ether were taken and cooled in a freezing mixture. Nitroso-methyl urea (1 g) was then added to the cold solution in small portion with shaking. The layer turned yellow due to formation of diazomethane. The aqueous layer was separated from the non-aqueous layer and washed with ice-cold water.

Part-D : Methylation (esterification) of samples : Methylation of authentic ABA and extracted ABA was done according to Ross and Bradbeer (349). One ml of precooled ether solution of extracted ABA was treated with 10 ml of diazomethane for 10 min. Solid ester of ABA separated out as precipitate.

The excess solution was evaporated at room temperature ($25 \pm 2^{\circ}\text{C}$) and then used for GC.

Samples were then identified and estimated by GC using the methyl ester of both extracted and authentic ABA (441). The cis-trans ABA (Sigma Chemical Co.) was used as authentic sample. The methyl esters were dissolved in a small volume of methanol and 5 μl of the solution was used for GC in Pye Unicam GC (Pye series 104) fitted with flame ionising detector device. The GC was done at the Bose Institute, Calcutta. The glass column (length 125 cm, internal diameter 1/4 cm) was packed with 5% SE-30 coated on 80-100 mesh acid washed and AW-DMCS treated chromosorb W. The column was preconditioned overnight at 300°C . Injector and detector temperatures were maintained at 190°C and 212°C , respectively. The nitrogen gas flow rate was 40 ml/min (used as a carrier gas). The amount of ABA present in the sample was determined by comparing the peak area percentage with the standard.

2.2.6.12.2. Cytokinin-like substances :

Fresh 70 g leaf samples were homogenized with 80% methanol (10 ml/g) and cytokinin-like substances were extracted following the method of Obata-Sasamoto and Suzuki (301). The extract was kept at 3°C for 24 hours. The methanol was filtered and the residue was extracted again with methanol. Pooled methanol was centrifuged at 15,000 rpm for 10 min and

the supernatant was evaporated in vacuo at 30°C. The pH of the aqueous phase was adjusted to 2.5 with 1 N HCl and washed 3 times, each time with 1/3 volume of methylene chloride. The aqueous phase again adjusted to pH 8 with 5% NaHCO₃ and extracted with 1/3 volume of water-saturated butanol. The extraction was repeated thrice. The pooled butanol was evaporated in vacuo at 28 ± 3°C. The residue was dissolved in 0.5 ml NaOH (0.05 N) and used for further purification chromatographically (TLC).

Purification of cytokinin-like substances : The extracted cytokinin-like substances (CK) were spotted on TLC plates (activated) along with authentic samples. The plates were then developed in solvent system (n-butanol:acetic acid:water = 4:1:1). The plates were then observed under UV lamp and all the fluorescent spots of authentic and extracted samples were marked. The R_f zones equivalent to authentic samples were scraped off from the TLC plates and eluted thrice with 80% methanol keeping at 5°C for 12 h. The extract was then used for determination of biological activity.

Bioassay of extracted CK-like substances : The cytokinin-induced chlorophyll formation in cucumber cotyledons (106) was used for testing the biological activity and estimation of CK-like substances of the extracted samples. The cucumber seeds (Cucumis sativa cv. Long green) were germinated in the

dark at $26 \pm 2^{\circ}\text{C}$ for 4 days. The cotyledons were excised and placed in a small Petridish (2" diameter) containing 3 ml of test solution. The Petridishes were first incubated in darkness for 14 h ($26 \pm 2^{\circ}\text{C}$) and then placed under the fluorescent lamp ($20 \mu\text{mol.m}^{-2} \text{sec}^{-1}$). The above experiment was repeated with 3 ml of kinetin solution (used as a standard), concentration ranging from 0.001 to 0.1 mg.lit^{-1} which gave a linear response (106). After 24 h the chlorophyll of the cotyledons was extracted in methanol (10 ml) and the chlorophyll concentration was estimated (11). By comparing the absorbancy of the chlorophyll induced by the authentic cytokinin (kinetin), the amount of CK-like substances in the extract was determined.

2.2.6.12.3. Ethylene :

The evolution of ethylene was measured colorimetrically following the method of LaRue and Kurz (200) with slight modifications. Five hundred mg leaf samples were taken in a well stoppered vial, and to it 1.5 ml of oxidant solution (50 ml 0.05 M NaIO_4 + 10 ml of 0.005 M KMnO_4 , pH 7.5) was injected. The vial was made partial air free with the help of a syringe and agitated vigorously on a rotary shaker for about 3 h at room temperature. Then 0.25 ml of 4 N sodium arsenate and 0.25 ml of 4 N H_2SO_4 were added to the vial to destroy the excess oxidant. One ml of Nash reagent

(150 gm of ammonium acetate + 3 ml acetic acid + 2 ml acetylacetone, diluted up to a liter) was added with the above solution. After one hour, a yellow coloration appeared and the absorbance was measured at 412 nm in a Spectrochem spectrophotometer. In the same way, a standard curve was prepared with ethrel.

The content of ethylene in the ethrel was determined by gas chromatography (Column 'Porapack N', oven temperature 80°C, detector and injector temperature 100°C, nitrogen used as the carrier gas, flow rate 40 ml/min. This was done at the Botany Department, Kalyani University, West Bengal through courtesy of Prof.S.P.Sen). One ml of concentrated ethrel contained 1.6207 ml ethylene gas. The amount of ethylene released by the sample was determined by comparing it with the standard curve of ethrel (where ethylene content was already been measured by GC).

2.2.7. Statistics :

The field experiments were repeated thrice, i.e., in a particular season of three different years. Biochemical parameters were analysed by taking six replications in each set of experiments and the data were incorporated in tables and figures.

The data included in tables were statistically analysed for LSD values at 95% confidence limits at the treatment and replication levels (314). The data which are presented in percentage were transformed into angular variances [\sin^{-1} transformation of Fisher and Yates (105)] and the statistical representations were made according to the above method. The standard errors around the mean were calculated (67) and plotted in figures.

R E S U L T S

2.3.1. Study of the pattern of leaf senescence of six rice and two wheat cultivars :

2.3.1.1. Study of the pattern of leaf senescence in terms of chlorophyll and protein contents and percentage of yellowing patches of total leaf :

The leaf senescence behaviour of the flag, second and third leaf of six rice and two wheat cultivars was studied in terms of decline in chlorophyll and protein contents with the progress of reproductive development and the results have been presented in Figures 1 to 3. The chlorophyll and protein contents of the flag, second and third leaf gradually decreased in all the rice and wheat cultivars. In short-statured Rasi and Sashyasri rice cultivars, the levels of chlorophyll (Figure 1) and protein (Figure 2) were greater in the flag leaf than in the second and third leaf until the grain maturation stage (21 DAA) , but at the senescent stage (28 DAA) the reverse trend was noted, where the levels of above components were greater in the older second leaf than in the younger flag leaf. On the other hand, in medium-statured Kalojira and Badsabhog rice cultivars, the loss of chlorophyll (Figure 1)

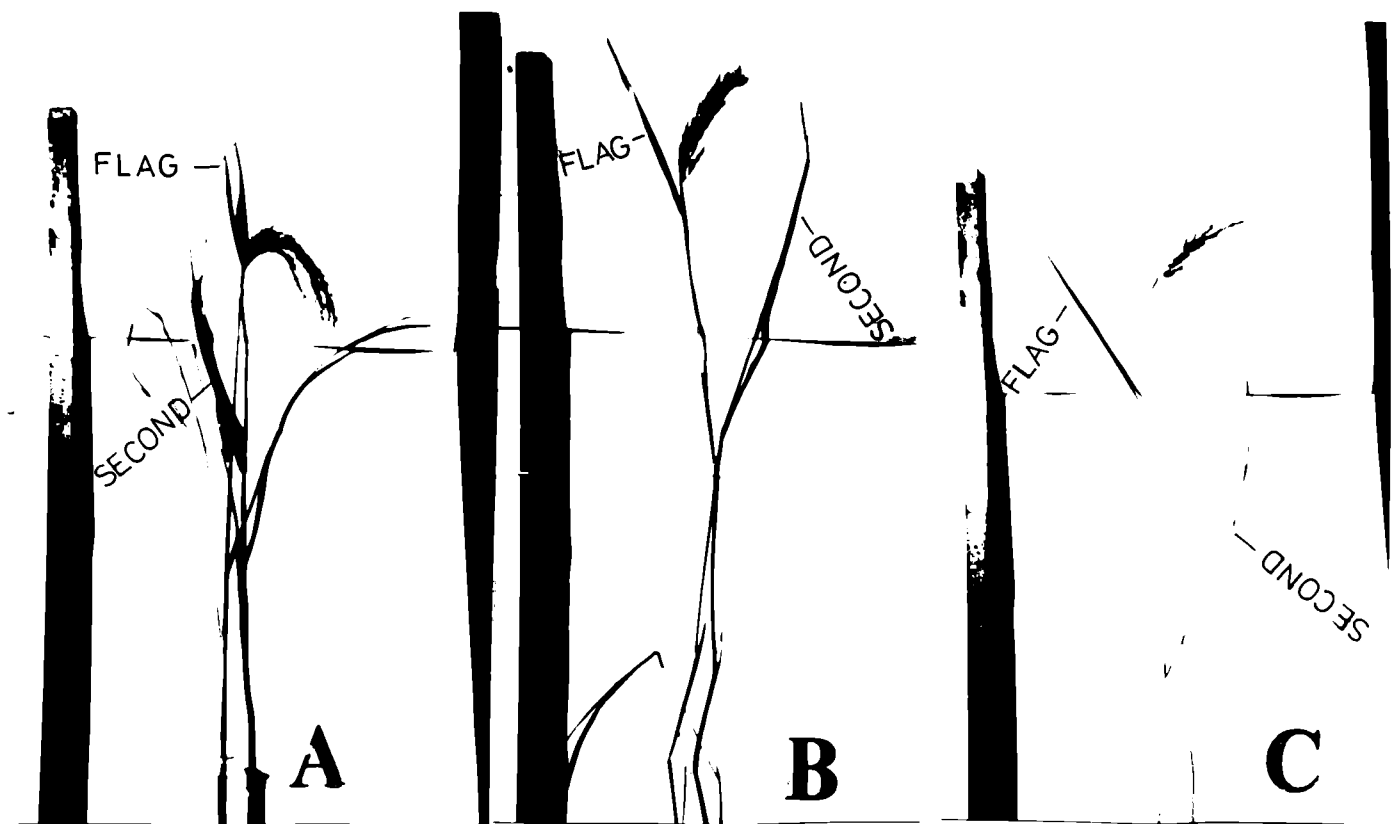
and protein (Figure 2) of the leaves was related to the chronological age of the leaf i.e., the flag leaf always contained greater level of chlorophyll and protein than the older second and third leaf throughout the reproductive development. However, in the tall Patnai and Kalma rice cultivars, the flag leaf contained higher levels of chlorophyll and protein than the second leaf up to the grain maturation stage but at the senescent stage the loss of above substances was more extensive in the flag than in the second leaf and their levels become almost equal in both flag and the second leaf at the senescent stage. As in medium-statured rice cultivars, in Sonalika and Kalyansona wheat cultivars, the loss of chlorophyll and protein (Figure 3) was related to the chronological age of the leaf and their levels were always higher in the younger flag leaf than in the more aged second and third leaf. In all the rice and wheat cultivars, the degradation of chlorophyll and protein was most extensive in the third leaf.

It was observed (Figures 4 & 5) that the area of second leaf of Rasi and Sashyasri rice cultivars was almost double that of the flag leaf, whilst this was almost equal in the two uppermost leaves of medium-statured Kalojira and Badsabhog rice cultivars. But in the tall Kalma and Patnai rice cultivars the area of the second leaf was slightly larger than that of the flag leaf. As in Patnai and Kalma, the area of the second leaf in Sonalika and Kalyansona

wheat cultivars was slightly greater than that of the flag leaf (Figures 6 & 7). It was observed that the onset of senescence or yellowing started earlier in the second leaf than in the flag leaf in all the rice and wheat cultivars (Figures 4 & 6). The yellowing patches of the flag leaf of Rasi and Sashyasri cultivars remained smaller than that of the second leaf up to the grain maturation stage (21 DAA), but an opposite picture was observed at the senescent stage (28 DAA, Plate 1A & B). In medium-statured Kalojira and Badsabhog rice cultivars, these patches were greater in the second leaf than in the flag leaf throughout the reproductive development (Plate 1C & D). Whereas, in tall Patnai and Kalma rice cultivars, yellowing patches were greater in the second leaf than in the flag leaf up to the grain maturation stage (21 DAA), but these were more or less equal at the senescent stage (28 DAA, Plate 1E & F). In Sonalika and Kalyansona wheat cultivars (Figures 6 & 7) such development of yellowing patches was proportional to the chronological age of the leaves and always greater in the second leaf than in the flag leaf throughout the reproductive development.

2.3.1.2. Changes in the contents of nitrogen and phosphorus in the leaves :

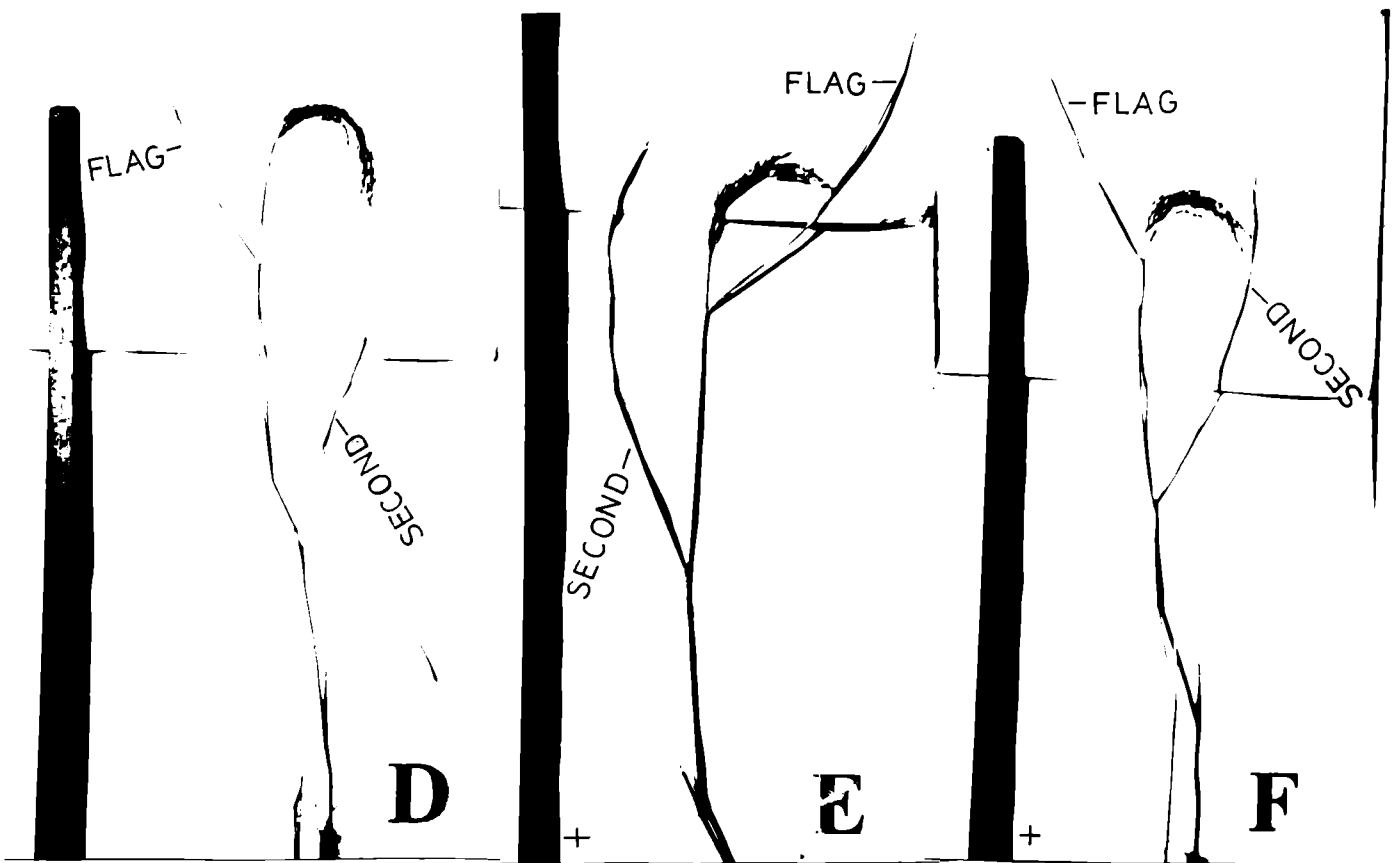
Changes in the contents of mineral nutrients, viz., nitrogen and phosphorus, were measured in the flag, second



RASI

SASHYASRI

BADSABHOG



KALAJIRA

KALMA

PATNAI

Plate 1

and third leaf of three rice and one wheat cultivars during the progress of their reproductive development and the results have been incorporated in Figures 8 & 9. The contents of nitrogen and phosphorus in all three uppermost leaves of rice and wheat cultivars gradually decreased during the progress of their reproductive development, but drastically so at the later stage (14 to 28 DAA). In Rasi, the decline of above mineral nutrients was larger in the flag leaf than in the second leaf at the grain maturation (21 DAA) and senescent (28 DAA) stages. Thus, at the senescent stage, their contents were greater in the second leaf than in the flag leaf (Figures 8 & 9). Whereas, in medium-statured Kalojira rice and Sonalika wheat cultivars, the decline in nitrogen and phosphorus from the leaves took place in accordance with their chronological age and more pronounced decline was noticed in the older second leaf than in the younger flag leaf. In tall Patnai rice cultivar, the decline of these nutrients took place at almost equal pace from the flag and the second leaf.

2.3.1.3. [³²P]-phosphate mobilization from leaves to grains:

The pattern of [³²P]-phosphate mobilization from (Figures 10 & 11) the flag, second and third leaf to the seeds and their retention (Figure 12) were recorded in three rice and one wheat cultivars during their progress of reproductive development. The export of [³²P]-phosphate from leaves to

grains varied between species as well as among cultivars. A greater amount of [^{32}P]-phosphate export was noted in rice cultivars in comparison with the wheat cultivar. Among the rice cultivars this was maximal in tall Patnai followed by Kalojira and Rasi. In all the rice and wheat cultivars, the maximal mobilization of [^{32}P]-phosphate to the panicle was observed from the flag leaf and minimal from the third leaf. The mobilization of [^{32}P]-phosphate from all the leaves gradually increased reaching the maximal level at the grain development stage (14 DAA) and declined thereafter (Figure 10).

In Rasi, the export of [^{32}P]-phosphate on unit leaf area basis, was much higher from the flag leaf than from the second and third leaf to the grains (Figure 11). In Kalojira, such difference in mobilization between the flag and the second leaf was less pronounced than that observed in Rasi. The mobilization of [^{32}P]-phosphate from the flag leaf on unit leaf area basis was larger in both Kalojira rice and Sonalika wheat cultivars. Among the rice cultivars, the export of [^{32}P]-phosphate was maximal in Rasi and minimal in tall Patnai cultivar. In Sonalika wheat cultivar, the mobilization of [^{32}P]-phosphate per unit leaf area basis was maximal from the flag and minimal from the third leaf (Figure 11).

It was observed that [^{32}P]-phosphate retention capacity (per leaf basis) of the fed leaves gradually decreased during the reproductive development of rice and wheat cultivars (Figure 12). In Rasi, the retention was greater in the flag leaf than in the second leaf up to the grain development stage (14 DAA), but this was reversed at the grain maturation stage (21 DAA), being greater in the second leaf than in the flag leaf. Whereas in Kalojira rice and Sonalika wheat cultivars, the retention capacity was always greater in the flag leaf than in the second leaf throughout the reproductive development. In Patnai rice cultivar, the retention capacity was marginally greater in the flag than in the second leaf at the senescent stage (28 DAA). The pattern of retention of [^{32}P]-phosphate by different leaves of Kalojira rice and Sonalika wheat cultivars was identical. The isotope retention capacity was maximal in Patnai and minimal in Rasi.

The total weight of panicle was separately recorded in all the rice and wheat cultivars (Table 1). Among rice cultivars, the panicle weight was maximal in tall Patnai and minimal in short-statured Rasi rice cultivar. In both medium-statured Kalojira rice and Sonalika wheat cultivars, the panicle weight was slightly greater than that in Rasi rice cultivar.

2.3.1.4. [^{32}P]-phosphate mobilization from roots to leaves and grains :

The pattern of [^{32}P]-phosphate mobilization from roots to the flag, second and third leaf and to the seeds during

the progress of reproductive development of three rice and one wheat cultivars was represented in the Figure 13. The mobilization of [^{32}P]-phosphate from roots to leaves and seeds gradually declined during progress of reproductive development of each cultivar and this was more marked in rice than in wheat cultivars. In Rasi, the export of [^{32}P]-phosphate from roots to the second leaf remained greater than that of the flag leaf throughout the reproductive development, whereas in Kalojira, this was significantly greater to the flag leaf than to the second leaf at the grain development (14 DAA) and senescent stage (28 DAA). Among the rice cultivars, maximal export of [^{32}P]-phosphate from roots to the leaves was recorded in Patnai and minimal in Rasi rice cultivar. In Patnai, the export of [^{32}P]-phosphate from roots to the second leaf was slightly larger than that to the flag leaf until the grain maturation stage (21 DAA) but at the senescent stage (28 DAA) it was reversed, being marginally higher to the flag leaf than to the second leaf. It was noticed that degree of decline of [^{32}P]-phosphate mobilization from roots to leaves was greater in Patnai than in the other two rice cultivars. In Sonalika wheat cultivar, the mobilization of [^{32}P]-phosphate from roots to the flag leaf was larger than that of the second leaf at the grain development (14 DAA) and senescent (28 DAA) stage. In all the rice and wheat cultivars, mobilization of [^{32}P]-phosphate to the seeds gradually decreased during the progress of reproductive development.

2.3.1.5. Correlation of leaf senescence patterns with xylem parameters at the juncture of leaf lamina and leaf sheath :

To elucidate the role of vascular bundles in facilitating mobilization of nutrients and hormones and its influence on nonsequential and sequential modes of leaf senescence behaviour, the number of vascular bundles at the juncture of leaf lamina and leaf sheath, area of the vessels in a bundle and the area of the lumen of the largest vessel were studied in the above rice and wheat cultivars and the results have been shown in Table 2. The number of vascular bundles, the area of xylem vessels in a bundle and the area of lumen of the largest vessel were variable among the leaves and between cultivars. These xylem parameters were greater in the second leaf than in the flag leaf in short-statured Rasi rice cultivar. On the other hand, these were almost equal in both the flag and the second leaf of medium-statured Kalojira rice cultivar (Table 2). But in tall Patnai, the above xylem parameters were marginally greater in the second than in the flag leaf (Table 2). The total number of vascular bundles and the area of xylem vessels in a bundle of the flag and second leaf of rice cultivars have been diagrammatically represented in Figure 14. In Sonalika wheat, the number of vascular bundles was more or less equal in both flag and second leaf but the area of xylem vessels in a bundle and that of the largest vessel were marginally greater in the second leaf than in the flag leaf (Table 2).

2.3.2. Effects of hormones on modification of the patterns of leaf senescence in rice and wheat cultivars

2.3.2.1. Study of effects of hormones on modification of the pattern of leaf senescence in rice and wheat cultivars in terms of decline in chlorophyll and protein :

Effect of benzyladenine (BA, 4.4×10^{-4} M), gibberellic acid (GA_3 , 2.9×10^{-4} M), abscisic acid (ABA, 7.5×10^{-5} M) and (BA + GA_3) [BA, 4.4×10^{-4} M and GA_3 , 2.9×10^{-4} M) on modification of leaf senescence behaviour of the flag, second and third leaf of two rice and one wheat cultivars representing the nonsequential and sequential modes of senescence (i.e., two extreme types) were studied in terms of decline in chlorophyll and protein contents and the results have been entered in Tables 3 to 6. BA treatment significantly increased chlorophyll and protein level of each leaf over the untreated control leaves in all these rice and wheat cultivars (Table 3). In Rasi, the application of BA maintained higher levels of chlorophyll and protein in the flag leaf than in the second leaf until grain maturation stage (21 DAA) but at the senescent stage (28 DAA), this was reversed. On the other hand, in Kalojira rice and Sonalika wheat cultivars, BA treatment maintained higher levels of chlorophyll and protein in the flag leaf than in the second leaf until the senescent stage. External application of GA_3 slightly retarded the loss of chlorophyll and protein in

all leaves of rice and wheat cultivars at all stages of reproductive development. However, retardation caused by GA_3 was significantly smaller than that by BA (Table 4). Also, GA_3 application like BA did not alter the pattern of leaf senescence of rice and wheat cultivars. ABA treatment, in general enhanced the loss of chlorophyll and protein in all three leaves of rice and wheat cultivars at all stages of reproductive development (Table 5). This effect of ABA became more prominent in the flag and second leaf during later stages of reproductive development (21 and 28 DAA). While in the third leaf, this became evident even at the grain development stage (14 DAA). In Rasi rice cultivar, ABA treatment did not alter the senescence pattern, and the second leaf always contained greater chlorophyll and protein than the flag leaf even at the senescent stage (28 DAA). This trend was also noted in Kalojira rice and Sonalika wheat cultivars, where the flag leaf always contained higher level of the above components than the second leaf throughout reproductive development. Treatment of leaves with a combination of (BA + GA_3) greatly augmented the chlorophyll and protein levels of three leaves in both rice and wheat cultivars (Table 6). The effect of the combined treatment of (BA + GA_3) was slightly greater than that of BA alone in all the cultivars of rice and wheat and the effect was most prominent at the later stages of reproductive development (14 to 28 DAA). However, above treatments did not alter the mode of leaf senescence of any cultivar.

2.3.2.2. Effects of hormones on nitrogen and phosphorus contents of leaves :

Effect of foliar application of BA, GA₃, ABA and (BA + GA₃) on changes in nitrogen and phosphorus contents of the flag, second and third leaf were studied and the results have been incorporated in Tables 7 to 10. Application of BA markedly arrested the decline of nitrogen and phosphorus contents in all three leaves of rice and wheat cultivars (Table 7) and the effect became more evident after the grain development stage (14 DAA). The increase over control in the contents of these nutrients due to BA treatment was more pronounced in the flag than in the second leaf in Rasi rice cultivar, whereas in Kalojira rice and Sonalika wheat cultivars, the increase in the contents of nitrogen and phosphorus was slightly greater in the second than in the flag leaf due to BA treatment. Application of GA₃ also slightly inhibited the loss of nitrogen and phosphorus in all the leaves of rice and wheat cultivars. The retarding effect of BA application on nutrient loss was, however, greater than that of GA₃ (Table 8). Contrary to the effect of BA and GA₃, ABA application accelerated the loss of above nutrients from the leaves of rice and wheat cultivars at all stages of their reproductive development (Table 9), and the effect was more spectacular after grain development stage (14 DAA). It was noted that a combined treatment of (BA + GA₃) strongly retarded the loss of

above nutrients from the leaves in all rice and wheat cultivars (Table 10). None of the hormones, when applied alone or in combination, did alter the pattern of the loss of nitrogen and phosphorus from the leaves in both rice and wheat cultivars (Tables 7 to 10).

2.3.2.3. Effect of treatment of BA and ABA on [^{32}P]-phosphate retention by and export from leaves to grains :

BA treatment augmented translocation of [^{32}P]-phosphate from the flag, second and third leaf to the grains of all the rice and wheat cultivars during reproductive development (Table 11). BA strongly augmented the export of [^{32}P]-phosphate from the flag leaf to the seeds in all the cultivars and such export was larger from the flag than that from the second leaf. Along with the augmentation of export of [^{32}P]-phosphate, BA also increased the retention capacity of each of the fed leaf (flag, second and third) of all the cultivars, which became most pronounced at the later stages of reproductive development (Table 11). BA greatly increased the retention capacity of the flag leaf of Rasi rice cultivar and of the second leaf of Kalojira rice and Sonalika wheat cultivars. On the other hand, ABA treatment produced an effect opposite to that of BA, which not only reduced the export of [^{32}P]-phosphate but also the retention capacity of the isotope in all the rice and wheat cultivars (Table 12).

2.3.3. Some senescence related biochemical and enzymatical changes in the leaves during reproductive development of rice and wheat cultivars and effects of hormones on them :

Changes in the contents of RNA, histone protein and the ratio between RNA and histone in the flag, second and third leaf of two rice (Rasi and Kalojira) and one wheat cultivars (Sonaliika) were recorded along with the effects of application of BA and ABA on them with the progress of reproductive development and the results have been represented in Figures 15 and 16 and Table 13. The histone level gradually increased, while the RNA level and the ratio between RNA and histone gradually decreased in the flag, second and third leaf in both rice and wheat cultivars (Figures 15 & 16) and the decrease was most pronounced at the grain maturation (21 DAA) and senescent stage (28 DAA). The decrease in RNA and the ratio between RNA and histone at the senescent stage was faster in the flag leaf than in the second leaf in Rasi. Whilst in Kalojira rice and Sonaliika wheat cultivars, these parameters decreased at a faster rate in the second leaf than in the flag leaf. On the other hand, histone protein content increased concomitant with the decrease in RNA content. The largest increase in histone protein was observed in the third leaf of each cultivar. Also, the maximal rise in histone protein level in each leaf was recorded at the senescent stage (28 DAA).

Foliar application of BA strongly inhibited the decrease in the RNA and the ratio between RNA and histone and increase in the histone protein content in all the leaves of rice and wheat cultivars. Such treatment also maintained a greater level of RNA and a higher ratio of RNA/histone and a lesser level of histone protein in the leaves compared with that of untreated control plants (Table 13). The marked effect of BA was observed after grain development stage (14 to 28 DAA). On the other hand, ABA treatment gave an opposite effect, i.e., strongly promoting the loss of RNA, lowering the ratio of RNA/histone and increasing histone protein level in all the leaves of rice and wheat cultivars (Table 13). Like BA, its effect was more pronounced at the later stages of reproductive development.

The accumulation of free amino acids gradually increased in the flag and second leaf up to the grain maturation stage (21 DAA) but slightly decreased at the senescent stage (28 DAA) in all the rice and wheat cultivars (Figure 17). But in the third leaf of these cultivars, such accumulation increased only up to the grain development stage (14 DAA), decreasing thereafter. However, in Sonalika wheat cultivar, the maximal accumulation of free amino acids occurred in the third leaf at the grain-filling stage (7 DAA), decreasing thereafter. In Rasi rice cultivar, the maximal accumulation of amino acids was observed in the flag leaf at the grain maturation stage (21 DAA), whereas this was maximal in the second leaf

in Kalojira rice and Sonalika wheat cultivars. Concomitant with the rise in free amino acid accumulation, the protease activity also increased gradually in all the leaves of both rice and wheat cultivars (Figure 18). The maximal increase was recorded in the third leaf at the senescent stage (28 DAA) of all the cultivars. The protease activity of the flag leaf of Rasi was greater than that of the second leaf only at the senescent stage. However, the activity of this enzyme showed an opposite trend in the flag and second leaf of Kalojira rice and Sonalika wheat cultivars, where the protease activity increased in the leaves according to the chronological age of leaves.

BA treatment significantly retarded the rise in free amino acid accumulation as well as protease activity in all the leaves of rice and wheat cultivars (Table 14). Such effect of BA was maximal at the grain maturation and senescent stage. ABA, on the contrary, markedly promoted the rise in free amino acid accumulation as well as protease activity in all the leaves of rice and wheat cultivars, but its effect was maximal at the grain maturation and senescent stage (Table 14). In both these treatments, the effect was maximal in the flag leaf of Rasi rice cultivar and in the second leaf of Kalojira rice and Sonalika wheat cultivars.

Changes in malondialdehyde (MDA) content and activities of superoxide dismutase (SOD) (Figure 19), catalase and

peroxidase (Figure 20) in the flag, second and third leaf of two rice (Rasi and Kalojira) and one wheat (Sonalika) cultivars were recorded during their reproductive development. The MDA (a product of oxidation of membrane polyunsaturated fatty acids) content increased gradually in all the leaves of rice and wheat cultivars, reaching a maximal level at the grain maturation (21 DAA) and senescent stage (28 DAA) (Figure 19). The maximal increase was noted in the third leaf at the senescent stage of all the cultivars, and minimal in the second and flag leaf of Rasi and Kalojira rice cultivars, respectively. The pattern of change of MDA in leaves of Sonalika wheat cultivar was similar to that of Kalojira rice cultivar. The activities of SOD (Figure 19) and catalase (Figure 20) gradually decreased in the leaves of both rice and wheat cultivars but maximal decrease took place in the third leaf in all these cultivars. The degree of decrease of the above enzymes at the senescent stage was greater in the flag leaf than in the second leaf of Rasi rice cultivar, but this was opposite in Kalojira rice and Sonalika wheat cultivars. On the other hand, the peroxidase activity (Figure 20) gradually increased in the flag and the second leaf of rice and wheat cultivars up to the grain maturation stage (21 DAA), but decreased at the senescent stage (28 DAA). In the third leaf of all cultivars, this enzyme activity gradually increased up to the grain development stage (14 DAA), declining thereafter.

External application of BA significantly arrested MDA production and increased the activities of SOD (Table 15), catalase and peroxidase (Table 16) in the leaves of rice and wheat cultivars. The effect of BA on the inhibition of MDA production and on the promotion of the activities of SOD (Table 15), catalase and peroxidase (Table 16) was maximal in the flag leaf of Rasi rice cultivar and in the second leaf of Kalojira rice and Sonalika wheat cultivars, respectively. On the other hand, ABA significantly augmented MDA production but inhibited SOD (Table 15), catalase and peroxidase (Table 16) activities. However, the effects of BA and ABA on these parameters were more prominent at the later stages of reproductive development.

2.3.4. Changes in the transpiration rate and proline accumulation during reproductive development of rice and wheat cultivars and effects of hormones on them :

Changes in the rate of transpiration and proline accumulation in the flag, second and third leaf and the effect of hormones on them during reproductive development of rice and wheat cultivars were shown in Figure 21 and Tables 17 to 19. The rate of transpiration was higher in Rasi than that in Kalojira rice cultivar and lower in wheat cultivar throughout the reproductive development. The rate of transpiration gradually decreased in all the rice and wheat cultivars with the progress of reproductive development. Transpiration rate

was maximal at the anthesis stage (0 DAA) and minimal at the senescent stage (28 DAA) (Table 17). It was noted that the rate of transpiration by a single leaf (when prevented in other leaves by vaseline smearing) of a plant was significantly greater than that of the whole plant. Like the whole plant, the rate of transpiration by each leaf also gradually decreased with the progress of reproductive development (Table 17). In Rasi, the rate of transpiration by the flag leaf was greater than that by the second leaf up to the grain maturation stage (21 DAA), but this trend was reversed at the senescent stage (28 DAA), when the rate of transpiration was greater in the second than in the flag leaf. However, in Kalojira rice and Sonalika wheat cultivars, the rate of transpiration was maximal by the flag leaf followed by the second and third leaf throughout the reproductive development (Table 17). Foliar application of BA significantly accelerated the rate of transpiration by the whole plant as well as by the single leaf, whilst ABA treatment inhibited the same in all the rice and wheat cultivars (Table 18). The effects of BA and ABA were most pronounced at the later stages of reproductive development. Such effect was maximal in the flag leaf of Rasi rice cultivar and second leaf of Kalojira rice and Sonalika wheat cultivars.

In contrast to transpiration rate, proline accumulation gradually increased in the flag, second and third leaf during reproductive development of rice and wheat cultivars

(Figure 21). In Rasi, proline accumulation increased in the leaves according to their chronological age up to the grain development stage (14 DAA) but this sequence was reversed at the grain maturation stage when the flag leaf contained the highest level of proline followed by the second and third leaf and this sequence was maintained up to the senescent stage (28 DAA). Unlike that in Rasi rice cultivar, in Kalojira rice and Sonalika wheat cultivars, the proline accumulation increased in the leaves proportional to the leaf age, i.e., higher accumulation in the older leaf than in the younger leaves took place up to the grain maturation stage (21 DAA) of the reproductive development.

Foliar application of BA significantly suppressed proline accumulation in all the leaves of rice and wheat cultivars throughout the reproductive development (Table 19). The effect of BA on the above parameter was most pronounced at the grain development stage (14 DAA) and continued up to the senescent stage (28 DAA). On the other hand, ABA treatment augmented proline accumulation in all the leaves of rice and wheat cultivars (Table 19). The effects of BA and ABA were greater in the flag leaf than in the second leaf at the senescent stage of Rasi rice cultivar, but in Kalojira rice and Sonalika wheat cultivars, an opposite trend was noted.

D I S C U S S I O N

Although a great deal of experimental results has been accumulated, the exact mechanism of monocarpic senescence, particularly at the molecular level, still remains unsettled. However, the evidence suggests that monocarpic senescence is correlatively controlled and there is no doubt that reproductive parts exert regulatory influence in the manifestation of monocarpic senescence. Among monocarpic plants, there are many different patterns in the relation of the time course of leaf senescence (287). In the present investigation, the patterns of leaf senescence have been studied in several rice and wheat cultivars in order to get an insight into the correlative control and the possible cause of monocarpic senescence in rice and wheat plants. To analyse the cause(s) of different patterns of senescence in these cultivars and to explore the role of mobilization of metabolites in the development of these senescence patterns, some physiological, biochemical, anatomical and hormonal studies were carried out in intact as well as surgically altered cultivars of rice and wheat.

Degradation is an essential feature of the senescence process and some quantitative measures are essential for understanding the developmental events occurring during

the senescence process. Previous studies from this laboratory indicated that the loss of chlorophyll and protein (32,35,257,339) and the loss of mineral nutrients, particularly nitrogen and phosphorus might serve as reliable indicators of the progressive senescence during reproductive development, at least in rice (256) and wheat (111) plants. Hence, in the present investigation the loss of above parameters was taken as indicators of senescence and an index of mobilization of metabolites from source to sink.

2.4.1. Studies in the leaf senescence behaviour of rice and wheat :

2.4.1.1. Two distinct modes of senescence patterns during whole plant senescence of rice and wheat cultivars have been reported (35,257). In the sequential mode of senescence the leaves senesce in a chronological order which means that leaf senescence is a function of leaf age. Whilst in the non-sequential mode, such age-related senescence could not be observed as in some rice cultivars, where the younger flag leaf senesces ^{longer} earlier than the older second leaf (257,339). The results of the present study with different rice and wheat cultivars reveal that the flag leaf of short-statured Rasi and Sashyasri rice cultivars demonstrated a nonsequential mode of senescence. Thus, there was a dramatic change in the decline of chlorophyll and protein in the flag leaf at the grain maturation stage (21 DAA). In these two rice

cultivars the loss of chlorophyll and protein and the percentage of leaf yellowing were larger in the flag leaf than in the second leaf (Figures 1,2 & 4), And they became more prominent at the senescent stage (28 DAA). On the other hand, in medium-statured Kalojira and Badsabhog rice and Sonalika and Kalyansona wheat cultivars, a sequential mode of senescence was observed, where the loss of chlorophyll and protein and increase in percentage of leaf yellowing were proportional to the leaf age (Figures 1 to 6) and the higher metabolic activity in terms of maintenance of chlorophyll and protein was noted in the younger flag leaf than in the older second leaf. These observations further confirm the earlier findings from this laboratory (257, 258), But the present study also included two other rice cultivars which showed an intermediate mode of leaf senescence. Thus, in tall-statured Patnai and Kalma rice cultivars, the loss of chlorophyll and protein and the percentage of leaf yellowing were more or less equal in the flag and the second leaf at the senescent stage and the two leaves senesced almost simultaneously (Figures 1,2 & 4). Hence, these two rice cultivars could not be categorized under either sequential or nonsequential mode as reported earlier and they showed an intermediate mode. The existence of these different patterns of leaf senescence in rice and wheat cultivars indicates that the senescence signal or death hormone may not be involved in inducing different patterns of leaf senescence in these cereal cultivars.

There is a distinct delimitation between reproductive parts and vegetative parts in cereals, and thus, any signal or death hormone originating in the panicle and moving downward would have first induced senescence in the nearest flag leaf in all the cultivars of rice and wheat reported here. Had it been the case, all rice and wheat cultivars would have shown a nonsequential mode of senescence, i.e., the flag leaf would have invariably senesced first regardless of species and cultivars due to its closest proximity to reproductive parts. But this was not true. The fact that both sequential and intermediate modes of leaf senescence also occur in rice and wheat cultivars apparently suggests that the senescence signal was not coming from the panicle, at least in rice and wheat cultivars.

2.4.1.2. If it is assumed that nutrients are mobilized from the nearer leaves to the developing seeds, there will be a gradual decrease of the mineral status of leaves during the progress of reproductive development. Also, a correlation between declining mineral status and the leaf senescence may be expected if deprivation of minerals and metabolites is governing the manifestation of senescence syndrome. In fact, the present study, where two most important mobile nutrients, nitrogen and phosphorus, were taken as indicators of mineral status of leaves (256), points in that direction. Thus, in short-statured Rasi rice cultivar, which represents

a non-sequential mode of whole plant senescence, the loss of these nutrients was more pronounced in the flag than in the second leaf at the senescent stage (28 DAA) (Figures 8 & 9). Interestingly, an opposite trend was observed in medium-statured Kalojira rice and Sonalika wheat cultivars, which are representatives of sequential mode of whole plant senescence. In fact, in these cultivars the loss of nitrogen and phosphorus in the three uppermost leaves below the panicle was exactly proportional to their leaf age (Figures 8 & 9). On the other hand, in the tall Patnai rice cultivar, which represents an intermediate type, the loss of these nutrients is more or less equal in the flag and the second leaf of different maturity status. Although Derman et al. (89) observed transfer of nitrogen from leaves to fruits in soybean before visible leaf yellowing, they failed to correlate such withdrawal of nutrients with the onset of senescence in soybean. However, the present study clearly reveals that loss of nutrients such as nitrogen and phosphorus from the leaves could be well correlated with the patterns of whole plant senescence in different rice and wheat cultivars. These results, thus, seem to suggest that loss of nutrients from leaves exerts regulatory influence on the manifestation of different modes of senescence observed in different rice and wheat cultivars.

2.4.1.3. To elucidate further the possible relation between mobilization of nutrients from leaves to grains and modes of leaf senescence demonstrated by different rice and wheat cultivars, the pattern of [^{32}P]-phosphate export from leaves to grains and retention of the same by the fed leaves were analysed. Apparently, the data favour the view that mobilization of nutrients from leaves to grains is an important factor in determining different modes of senescence manifested by different rice and wheat cultivars. The export of [^{32}P]-phosphate per leaf basis was significantly greater from the flag than from the second leaf in all the rice and wheat cultivars, which reached a maximal point at the grain development stage (14 DAA), declining thereafter (Figure 10). This suggests that flag leaf is the main exporter of nutrients to the grains, perhaps due to its greater proximity to the sink (Figure 10). When measured per unit leaf area basis (Figure 11), the export of [^{32}P]-phosphate was maximal from the flag leaf of Rasi followed by that of Kalojira rice and Sonalika wheat and Patnai rice cultivars. The leaf area data depicted in Figure 4 further reveals that the export of [^{32}P]-phosphate was inversely proportional to the area of the flag leaf in different cultivars. The area of the flag leaf of Rasi was minimal, but the export of phosphate isotope was ~~also~~ maximal in this cultivar. However, this was just opposite in other cultivars. Thus, the flag leaf of Rasi undergoes greatest nutrient deprivational stress at the

grain development stage (14 DAA) and registered the earliest senescence syndrome. Conceivably, the difference in export between the flag and the second leaf was more pronounced in Rasi than in either Kalojira or Patna1 and the difference was much less in the latter cultivars suggesting that both the flag and the second leaf equally participated in the process of nutrient export and the second leaf, being older than the flag leaf, senesced earlier. The pattern shown by Sonalika wheat cultivar exactly followed the same trend as that in Kalojira. Working with the Vigna radiata, Rao and Ghildiyal (335) have suggested that sink itself is instrumental in hastening the declining photosynthesis and the leaf senescence by effecting directly the mobilization and reutilization of nitrogen. The results of the present study also suggest that leaf became exhausted owing to increasing sink demand of the developing grains.

The data of retention capacity of [^{32}P]-phosphate of fed leaves (Figure 12) reveal that the isotope retention capacity remained greater in the second leaf than in the flag leaf of Rasi even at the senescent stage. This suggests that the metabolic activity remained greater in the second than in the flag leaf of this cultivar at the senescent stage. On the other hand, the capacity for retention of [^{32}P]-phosphate in Kalojira rice and Sonalika wheat was identical and always greater in the flag than in the second leaf which was in accordance with the maturity status of the

leaves (Figure 12). However, in Patnai, although the pattern of retention of phosphate isotope was similar to that of Kalojira rice and Sonalika wheat cultivars particularly at the earlier stages of reproductive development, the retention capacity of the isotope by both flag and second leaf of this cultivar became more or less equal at the senescent stage (Figure 12). If we consider [^{32}P]-phosphate retention capacity as an indicator of leaf metabolic activity, it will be evident that the retention capacity was proportional to the leaf maturity status in the cultivars Kalojira rice and Sonalika wheat, which were showing sequential mode of senescence. Interestingly, the situation was quite opposite in Rasi showing non-sequential mode of senescence. In the cultivar Patnai, where both the flag and the second leaf senesced almost simultaneously, also registered an equal [^{32}P]-phosphate retention capacity by the flag and the second leaf.

If we cast a glance at the [^{32}P]-phosphate mobilization data shown in Figure 10, it will be revealed that the export of [^{32}P]-phosphate from the leaves was greatest in Patnai followed by Kalojira and Rasi and least in Sonalika. That this export was directly proportional to the sink strength can be substantiated from the data of total weight of panicle in different cereal cultivars studied (Table 1). Thus, it is clear from the data that among the rice cultivars the export of [^{32}P]-phosphate was maximal in Patnai where the

sink strength (panicle weight) was also maximal. On the contrary, the export of [^{32}P]-phosphate from leaves to grains was minimal in Rasi where the sink strength was also minimal. These results thus suggest that sink demand of different rice and wheat cultivars exerts a regulatory influence on the export of nutrients from leaves. Whether active sinks, such as developing fruits, function only in a passive manner by consuming soluble nutrients thereby driving a mass flow system (73) or whether sinks send some hormonal regulatory signals to the supply organs to regulate their activity (289, 290) cannot be said from these results with certainty. Nevertheless, it is certain that the rate of senescence has a relationship with mobilization of nutrients which seems to be proportional to the sink size in rice and wheat cultivars. MacKown et al. (218) have recently reported that labelled N in wheat is translocated to the reproductive parts according to the sink strength and this is in full agreement with the [^{32}P]-phosphate export data presented here.

2.4.1.4. It is well known that supply of water, mineral nutrients and cytokinins from roots to leaves influences the rate of senescence (115,276,278,450). During monocarpic senescence in soybean several authors have shown that root growth ceases, degenerative changes occur and net mineral accumulation declines (89,281,283). Roots generally provide

cytokinins and minerals required for maintenance of foliar function and pod development. It has been suggested that changes in the rate of delivery of xylem solutes have regulatory effect on leaf senescence and regulate soluble protein and chlorophyll level (234), as also photosynthetic gas exchange and stomatal resistance (143). In the present study the export of [^{32}P]-phosphate from the isotope-fed roots to the leaves was taken as an indicator of mobilization of nutrients from roots to leaves. The data presented here reveal that there was a gradual decline in the export of [^{32}P]-phosphate from roots to leaves in all rice and wheat cultivars (Figure 13). An analysis of the pattern of mobilization of this isotope in Rasi rice cultivar shows that [^{32}P]-phosphate was exported significantly at a greater extent to the second than in the flag leaf and least so in the third leaf. Thus, not only greater export of metabolites from the flag leaf to the grains, but also lesser entry of nutrients (and possibly root-originated cytokinins) into this leaf might possibly be the major reasons for earlier senescence of the flag leaf than the second leaf. In contrast, the export of [^{32}P]-phosphate from roots was larger in the flag than in the second leaf (Figure 13) in Kalojira rice and Sonalika wheat cultivars and it seems clear that the flag leaf of these cultivars received greater supply of nutrients (and also cytokinins) from the roots compared with the second leaf which enabled it to acquire greater sustenance

capacity and hence senescing later than the second leaf. In Patnai rice cultivar, the export of [^{32}P]-phosphate from roots to the flag and the second leaf did not differ appreciably (Figure 13) and senesced almost simultaneously. The above results, therefore, point out that the supply of nutrients from roots to the leaves varies in different cultivars and possibly plays a role in modifying the leaf senescence behaviour. Such differential export patterns from roots to leaves not only seems to depend on the metabolic status of roots and leaves, but also on the vascular architecture of the specific plant concerned. This will be evident from the studies that follow.

2.4.1.5. To substantiate the above view, the number of vascular bundles at the juncture of leaf lamina and leaf sheath, the area of xylem vessels in a bundle and the lumen of the largest vessel were recorded in three rice and one wheat cultivars (Table 2). Kishitani and Tsunoda (1977) could obtain a positive correlation between total cross-sectional area of xylem vessel at the leaf base and leaf area with the photosynthetic rate and water supply. Thus, in short-statured Rasi rice cultivar, showing non-sequential mode of leaf senescence, the above xylem parameters were greater in the second than in the flag leaf and the data of the previous experiments also provided evidence of greater nutrient supply to this leaf. It can, therefore,

be concluded that supply of nutrients (and also cytokinins) from roots to leaves can be regulated and restricted by the vascular architecture prevailing at the juncture of leaf lamina and leaf sheath, which plays an important part in regulating leaf senescence behaviour of the plant. This will be further clear if we analyse the xylem parameters of Kalojira and Patnai rice and Sonalika wheat cultivars (Table 2) where the data of [^{32}P]-phosphate export from roots to leaves and the mode of leaf senescence could also be well correlated. It can be documented in the literature that the fibrovascular tissue system of a plant regulates supply of water, mineral nutrients and cytokinins from roots to the leaves which can eventually modify leaf senescence and that the hydraulic architecture of the shoot also plays a major role in the regulation of leaf senescence (269,273, 277,281,291).

2.4.2. Effect of phytohormones on whole plant senescence of rice and wheat :

2.4.2.1. It is well known that phytohormones as foliar sprays can modify senescence of leaves attached to the plant depending upon the species and leaf maturity status (32,35, 87,281,297,351,339). Among the phytohormones, cytokinins almost universally retarded senescence of leaves. Next to cytokinins, GA_3 has been found to retard senescence in many cases (249,272). However, auxin is the least effective

hormone in this respect (167). Nooden (285) also reported that a combination of (BA + GA₃) synergistically delayed senescence of soybean plants. On the other hand, ABA and ethylene promote senescence of the whole plant in a majority of the cases. In the present investigation, BA, GA₃ and their combination (BA + GA₃) and ABA were used as foliar sprays to examine their effects on the modification of non-sequential and sequential modes of senescence (two extreme types) as observed in rice and wheat cultivars. The study reveals that none of these hormones could change the pattern (i.e., non-sequential and sequential) of senescence characteristic of a particular cultivar. However, BA, GA₃ and their combination retarded senescence of all the leaves over their control, the combination treatment being most effective, whereas ABA accelerated senescence in these cultivars (Table 3 to 6). The most interesting feature of this study is that, although the hormones could modify the senescence of leaves, they failed to modify the pattern of whole plant senescence shown by a particular cultivar. It is to be noted that the application of BA, GA₃ and their combination (BA + GA₃) could reduce the difference in the contents of chlorophyll and protein between flag and second leaf in all the cultivars which became most pronounced at the senescence stage in untreated control plants. ABA treatment, on the other hand, markedly increased such difference in the levels of above cellular components in the flag and

second leaf over the untreated control plants in these cultivars (Table 5). It is noteworthy that effects of all these phytohormones, regardless of their senescence retarding or promoting effects, became evident only at the later stages of reproductive development suggesting that the sensitivity of attached cereal leaves to these phytohormones was much less at the earlier stages of reproductive development. It may be assumed that since the effects of these phytohormones on the total longevity of these plants were rather small, being only effective at the very late stage of reproductive development, they failed to impose any modification on the mode of whole plant senescence observed in these cultivars.

2.4.2.2. Since depletion of mineral nutrients from leaves during reproductive development is an important characteristic of monocarpic senescence (56,89,132,268,291,383), ^{may consider} it ~~will be~~ worthwhile to study the effects of above phytohormones on the changes in nitrogen and phosphorus contents of the leaves during the progress of reproductive development in rice and wheat cultivars (Tables 7 to 10). The study reveals^{ed} that the application of senescence retarding hormones, such as BA, GA₃ and their combination, also retarded the loss of these nutrients from the leaves in accordance with the senescence behaviour of leaves of each cultivar of rice and wheat (Tables 7 to 10). Expectedly, the senescence

promoting hormone ABA rather accelerated the loss of these nutrients, thereby creating greater depletion in the leaves and consequently their earlier senescence. Even though the application of these phytohormones could delay or accelerate the loss of nitrogen and phosphorus from leaves of these cultivars, they failed to alter the specific trend and pattern of depletion of these nutrients shown by the leaves of control plants of each cultivar. Thus, the depletion of these nutrients could be correlated with the mode of senescence displayed by a particular cultivar, notwithstanding that such depletion was either delayed or accelerated by phytohormone application.

2.4.2.3. In order to critically assess the role of senescence retarding and promoting hormones on mineral redistribution, the pattern of export of labelled phosphate from leaves to grains and the retention capacity of the leaves were studied in BA- and ABA-treated rice and wheat cultivars (Tables 11 & 12). The results reveal that BA significantly increased export of [^{32}P]-phosphate as well as the retention capacity of the fed leaves (Table 11), whereas ABA caused an opposite effect in all the cultivars (Table 12). It is interesting to note that although BA and ABA exerted an influence on the export and retention capacity of [^{32}P]-phosphate, the pattern remained essentially the same as that of leaves of untreated control plants in all these

cultivars. This is reminiscent of the observations made by Mondal and Choudhuri (257) in some other rice cultivars. The higher export and retention capacity of [^{32}P]-phosphate by the leaves treated with BA may be attributed to higher synthetic and metabolic activity of BA-treated leaves (91, 198,304,423), while the lower export and retention capacity of radiophosphate in ABA-treated leaves may be interpreted as due to lower metabolic activity and higher degradative processes induced by ABA in treated leaves (104, 289,304, 370).

2.4.3. Role of certain biochemical and enzymatical changes in the senescence development in rice and wheat :

It is now well recognized that gene action is mediated by gene products which characterize the particular tissues and particular stages of development (43,203). Thus, the appearance and then disappearance of gene products are characteristic features of developmental cycles (92). However, senescence is regulated by a set of genes acting in concert and it is a carefully orchestrated phenomenon resulting in the controlled dismantling of specific cell structures (43, 291,410,455). Implicit is the idea that senescence results from programmed changes in gene products. Results of the present study provide evidence of changing patterns of RNA and histone protein in different leaves of rice and wheat cultivars. These two biomolecules seem to

play an important role in the execution of programmed senescence (191,376,388). The present experiment shows that there was a decrease in RNA and increase in histone protein and decrease in the ratio between RNA and histone in the leaves of all the rice and wheat cultivars according to their mode of senescence (Figures 15 & 16). It may be emphasized that there exists an inverse relationship between changes in RNA and histone protein. And the decrease in the ratio of RNA/histone seems to be a consistent indicator of ageing and senescence rather than the changes in their individual component. Furthermore, their changes were most easily discernible prior to senescence of a particular leaf, implicating their active involvement in the senescence process. It is documented in the literature that chromosome-associated histone protein increases and RNA decreases during ageing and senescence of leaves (43,94,252,351,368,410,452,455) which further corroborates the present findings. Application of BA and ABA to the leaves on these cultivars appropriately modified these changes (Table 13), pointing-out their regulatory effects on genes and gene products associated with senescence development. It is now well known that histone protein inhibits the ability of DNA to serve as a template for RNA synthesis (180,204,390). Petel and Berlyan (317) have also shown a close relationship between DNA/histone ratio and RNA content, and the decrease in H1 histone has also been correlated with transcriptionally poised chromosome

structure (69). From the observations of decline in RNA and RNA/histone ratio and slow rise in histone protein in the leaves approaching senescence in different rice and wheat cultivars, it can be assumed that the major synthetic activities are perhaps gradually switched off and the degradative processes switched on during ageing and senescence.

Another spectacular manifestation of switching on of the degradative processes during ageing and senescence is the protein breakdown resulting from high protease activity and the consequent rise in free amino acids in leaf tissues. The liberated free amino acids along with other nitrogenous substances produced during senescence are eventually translocated to the developing grains to meet their demand for nitrogen assimilation (323). The present study also confirms this. The loss of protein in leaves of different rice and wheat cultivars could be correlated with the rise in protease activity with the concomitant accumulation of free amino acids. This was also found to be a function of senescence pattern of leaves. Thus, in the cultivar Rasi, which shows non-sequential mode of leaf senescence, the changes in protease activity and accumulation of free amino acids in leaves were also found to be non-sequential (Figures 17 & 18). Whereas, in the sequential mode of senescence, manifested by Kalojira rice and Sonalika wheat cultivars (Tables 17 & 18), their changes were also sequential, i.e., proportional to the leaf age. The greatest accumulation of free amino acids

in leaves due to proteolysis could be observed at the grain maturation stage, but there was a decline afterwards suggesting that both demands for nitrogen by the sink (panicle) and the supply by the source (leaves) are perhaps reduced prior to senescence. The maintenance of high protease activity until complete senescence of leaves might suggest that protein breakdown occurred till very late stage of senescence. However, lesser accumulation of free amino acids in leaves during this period may apparently appear to be conflicting, But this apparent contradiction may be interpreted as due to known involvement of free amino acids in the synthesis of different hydrolytic enzymes associated with senescence (396) and also in meeting the nitrogen demand of other vegetative parts which are yet to senesce (351).

The deferment of senescence by the application of BA and its promotion by ABA are also reflected in protease activity and free amino acid accumulation (Table 14), implicating a regulatory role of these phytohormones in protein turnover (289,423). Regardless of the particular pattern of senescence displayed and the initiating and controlling factors involved, the senescence of individual leaf of the cereal cultivars seems likely to be similar at the cellular level. And the present study is indicative of the fact that a balance between senescence retarding and promoting hormones at the cellular level may be one of the important controlling factors of senescence development.

Cellular membranes are selective, dynamic barrier that play an essential role in regulating biochemical and physiological events and the deterioration of membrane is an early fundamental feature of the senescence process (411). Thus, during senescence there is progressive loss in membrane integrity resulting in a rise in membrane permeability. Most of the proteolytic enzymes are known to be located in the vacuoles, while majority of the proteins are located in the chloroplasts (112,220,221,402,438). It follows, therefore, that membrane damage is necessary for protein breakdown and senescence development. It has been postulated by Veierskov and Thimann (424) that senescence process is facilitated by gradual impairment of vacuolar membrane, allowing proteases to enter into the cytosol and attack the proteins there and in the organelles. Free radical-mediated lipid peroxidation is an important mechanism causing membrane deterioration during senescence (411). The accumulation of free radicals during ageing and senescence is also known to augment lipid peroxidation, and one of the reasons for their accumulation is the gradual loss of activities of free radical scavenging enzymes such as superoxide dismutase (SOD), catalase and peroxidase. The present study with different cultivars of rice and wheat also supports the above hypothesis. Thus, there was senescence-related proportional increase in the level of malondialdehyde (MDA), which is the oxidation product of polyunsaturated membrane fatty acids and a reliable

indicator of membrane deterioration, in leaves of different rice and wheat cultivars (Figure 19) pointing out that membrane deterioration is the function of ageing and senescence in these cultivars. That such membrane deterioration is induced by free radicals can be indirectly substantiated from the observations of the decline in the activity of SOD and catalase in leaves with the approach of senescence (Figures 19 & 20) favouring accumulation of oxy free radicals which might lead to membrane deterioration. It has been amply demonstrated by a number of workers that H_2O_2 is the stable product of oxy free radicals generated in tissues (96) and the involvement of H_2O_2 in the senescence of leaves has been demonstrated in various plants (61). The rise in peroxidase activity during senescence along with H_2O_2 may also facilitate oxidative degradation of cellular macromolecules and such a rise in peroxidase activity was also noted in leaves of rice and wheat cultivars (Figure 20). The accumulation of MDA and changes in free radical scavenging enzymes were most pronounced at the senescent stage of rice and wheat cultivars. All these results seem, thus, to indicate that progressive loss of free radical scavenging enzymes, which favour accumulation of free radicals and H_2O_2 , may lead to membrane deterioration in leaf tissues and consequently senescence.

The external application of BA significantly retarded MDA accumulation and enhanced the activities of free radical scavenging enzymes (Tables 15 & 16) as mentioned above, while ABA caused an opposite effect. Thus, it may be assumed that one of the mechanisms of phytohormones retarding or promoting senescence of plant tissue is mediated by regulating free radical scavenging enzymes such as SOD, catalase and peroxidase and modulating free radical-induced lipid peroxidation and membrane damage.

2.4.4. Role of transpiration in the regulation of senescence:

Transpiration seems to play an important role in the regulation of monocarpic senescence because the supply of cytokinins, nutrients and water to the aerial parts is partly dependent on the transpiration pull along the stem axis (115, 157, 174, 281, 289, 384). The present study shows that rate of transpiration by the whole plant (main tiller) gradually decreased in rice and wheat cultivars during their reproductive development (Table 17). The rate of transpiration also decreased in accordance with the mode of senescence in these cultivars. Such decrease in the rate of transpiration may be related with age of leaves, since stomata are known to fully or partially close in aged tissue of many plants (403, 405). While treatment of plants with BA significantly increased the rate of transpiration by the whole plant as well as by

individual leaf, ABA spraying strongly inhibited the same in all the cultivars studied (Table 18). It is documented in the literature that cytokinins keep stomata open, while ABA causes stomata to close (160,171,231,333,403). The effects of BA and ABA in the present experiments can be interpreted on the basis of their regulatory influence on stomatal opening and closing. There are also reports that a decrease in cytokinins and an increase in ABA level take place during ageing and senescence in plants (85,118,300, 360,436). The occurrence of such a situation under natural condition may strongly favour stomatal closure that presumably be responsible for the reduction of transpiration in different rice and wheat cultivars during progressive ageing.

The accumulation of proline in stressed tissues is a widely reported observation (46,324,393,395). Proline accumulation during ageing and senescence has also been reported in isolated (394,430) as well as in intact leaves (260,392) of many species. Furthermore, it has been postulated by Biswas and Choudhuri (32) that mobilization of metabolites from leaves to grains in rice during reproductive development causes a deprivational stress in leaves. It was subsequently demonstrated by Ray and Choudhuri (339) that there was an increase in ABA-like substances due to such deprivational stress in rice leaves. That stress-induced ABA can, in turn, enhance proline accumulation in leaves is also well documented

(12,324,394). Like ABA, proline can also promote stomatal closure (333,334). Thus, the accumulation of both ABA and proline with ageing may serve as reliable indicators of whole plant senescence. In the present study it was observed that proline accumulation gradually increased in the leaves of all rice and wheat cultivars up to the grain maturation stage, but decreased thereafter (Figure 21). Thus, at the grain maturation stage maximal accumulation of proline took place in the flag leaf of Rasi, while it was in the second leaf in Kalojira rice and Sonalika wheat cultivars. These results fit in well with the observed modes of senescence in these cultivars. The maximal accumulation of proline at the grain maturation stage suggests that the leaves had undergone maximal stress prior to this stage. The data of [32 P]-phosphate export, discussed earlier (Figure 10), show that maximal mobilization of metabolites took place at the grain development stage. Thus, it may be assumed that the leaves were subjected to maximal deprivational stress at the grain development stage (14 DAA) and such an assumption finds support from the observation of proline accumulation at the grain maturation stage (21 DAA). Our data, therefore, lend further credence to the postulation made by Biswas and Choudhuri (32) as alluded before. A large number of reports shows that the application of ABA induces proline accumulation in the treated tissue (12,324,392,394). However, the effect of cytokinin on proline accumulation has been scarcely reported (260,395). Nevertheless, the retardation of proline

accumulation by BA and its acceleration by ABA treatment in leaves of rice and wheat cultivars (Table 19) suggest that proline accumulation is one of the characteristic features of senescence syndrome and may be intimately involved in the process of senescence development. From the evidence presented here it may be assumed that retardation of the accumulation of proline by BA and its promotion by ABA treatment may presumably be mediated by decreasing or increasing the internal nutrient deprivational stress, respectively.

2.4.5. Hormonal mechanism of regulation of senescence :

In recent years, several studies have emphasized the regulatory role of endogenous cytokinins and ABA in the senescence process of the whole plant or detached organs, particularly leaves (9,32,64,278,283,297,300,351,384,403,423). It is also well known that ethylene plays an important role in leaf abscission, but its role in leaf senescence is not very clear. Several workers, however, have suggested that ethylene acts as a senescence promoting hormone (1,5,119,176). It has also been demonstrated that during senescence the release of endogenous ethylene increases (15,176). Reports concerning the decrease in endogenous cytokinin-like (CK-like) substances and the rise in endogenous ABA level during ageing and senescence of leaf tissues are also not very uncommon in the literature (32,60,84,118,174,211,291,300,302,303,339,436). The present study with different rice

and wheat cultivars also supports the above findings. The study shows that CK-like substances gradually decreased in all the leaves of both rice and wheat cultivars during the progress of reproductive development (Figure 22). In Rasi, the decline in CK-like substances was much greater in the flag than in the second leaf. In contrast, an opposite trend was observed in Kalojira rice and Sonalika wheat cultivars. These findings are in complete agreement with the observed mode of senescence in these cultivars. In general, the decline in CK-like substances may presumably be ascribed to the decline in root cytokinin production (85, 184, 294, 300) which may also be correlated with lowering of transpiration pull (21, 115, 150). The little cytokinins that are still produced by the roots may be translocated to the developing seeds instead of leaves because of greater sink demand of the former (211, 287, 289, 357, 436). Such a view gets its support from the observation that depodding increases CK-level in leaves and delays senescence in soybean (300). The decline in cytokinin in leaves may be also responsible for inhibiting the synthetic processes and promoting the degradative processes (32, 35, 173, 174, 259, 289, 460).

Concomitant with the decline in CK-like substances in leaves, the level of ABA gradually increased up to the grain maturation stage, declining thereafter in rice and wheat cultivars (Figure 23). The decline in ABA in the flag leaf

of Rasi was faster than that in the second leaf. Whereas in Kalojira rice and Sonalika wheat cultivars, the level of ABA increased in chronological order of the leaves (Figure 24). Thus, earlier accumulation of ABA in the flag leaf of Rasi and in the second leaf of Kalojira rice and Sonalika wheat cultivars with the simultaneous decline in CK-like substances prior to senescence development appears to be an important factor regulating monocarpic senescence of cereal plants. The external application of these two hormones also exerted their regulatory effects on the whole plant senescence of these cultivars. The effect of ABA on the whole plant senescence may presumably be mediated through retardation of many physiological and biochemical processes such as photosynthesis, protein synthesis stomatal closure etc (118,134,289,291,345,351,370,403).

It is noteworthy that the ratio of CK-like substances and ABA gradually decreased with the progress of reproductive development in both rice and wheat cultivars. The maximal decrease was observed at the grain maturation stage (21 DAA), which just preceded the senescent stage (28 DAA). All these results seem, thus, to suggest that a critical balance between these two hormones has a profound regulatory influence on the development of monocarpic senescence in cereal plants. This is in complete agreement with the view of several workers (95,101,351). But it is not yet

clear from these results what actually triggers the initiation of monocarpic senescence in these plants.

Among the known hormones, the role of ethylene in whole plant senescence is most conflicting, although ethylene has been suggested by many workers to^{as} act as a senescence promoting hormone in attached and detached leaves of many species (1,5,176,241,332,458). Aharoni et al. (7) have reported that ethylene production decreased in the first phase of senescence and there was a transitory rise in ethylene production during the phase of rapid chlorophyll loss. From our data it could be stated that the release of ethylene was the function of leaf ageing and senescence development in different rice and wheat cultivars (Figure 25). Thus, with the approach of senescence, the release of ethylene also increased. The rise in ethylene production was significantly faster at the later stage of reproductive development in both rice and wheat cultivars. The difference in ethylene production between the flag and the second leaf of Kalojira (rice) and Sonalika (wheat) was not as prominent as that of Rasi. That ethylene plays a regulatory role in petal senescence has recently been demonstrated by Lawton et al (203) in carnation. It has also been reported by Woodson (448) that flower senescence in carnation is associated with changes in gene expression involving both protein and in RNA changes. The early rise in ethylene in leaves during anthesis stage suggests that ethylene might

also play a similar role in cereal leaf senescence as has been observed in carnation petals. One interesting finding reported by Schwabe and Kulkarni (366) is that severe water stress, which was accompanied by a significant rise in ABA in detached leaves of Kleinia articulata, did not lead to senescence unless combined with ethylene treatment and postulated that while ABA might play an important role in leaf senescence, its lethal effect could not be realised until and unless ethylene-induced membrane changes would also synergistically assist. External application of ethylene has also been reported to enhance various senescence-related processes in plants (176,313,447). From all these observations along with those reported here, it may be concluded that a decline in CK level and a rise in ABA and ethylene levels in plants during their reproductive development are intricately involved in the senescence development of different cereal cultivars.

2.4.6. Changes in nucleic acids and proteins in the shoot apex during transition from vegetative to flowering stage of rice and wheat cultivars :

It has been observed that the transition from the vegetative to the reproductive stage is accompanied by profound physiological, biochemical, genetical and hormonal changes in plants (25,78,126,131,164,165,195,217,371). Since developmental processes are genetically programmed, the gene products are also accordingly changed for the execution of

this programme. Evidently, characteristic changes are expected to occur in nucleic acids and proteins, the main biochemical agents for the execution of the developmental programme during transition from the vegetative to the reproductive stage. In the present study we, therefore, attempted to analyse changes in some important biomolecules deemed to be associated with such transition. Thus, changes in total protein, DNA, RNA and histone protein were studied prior to this transition in two rice and one wheat cultivars. There was a significant rise in protein, DNA and RNA in the shoot apex of Rasi rice cultivar up to the plant age of 74-80 days, i.e., at least 12 days before panicle emergence and there was a decline thereafter (Figure 26). Interestingly, the histone protein increased at the plant age of 77 to 80 days when other biomolecules started declining. The same trend was also noted in Kalojira rice and Sonalika wheat, varying only in the time period (Figures 27 & 28). Histone protein is known to act as an inhibitor of gene expression (180,388,390). The critical rise in nucleic acids and total proteins and decline in histone protein prior to transition from one phase to the other suggests that profound gene activity may possibly be required for panicle initiation in these cereal cultivars. The decline in nucleic acids and protein and the rise in histone protein perhaps mark the end of the transition phenomenon. From all these results it can be concluded that marked changes in genetic materials as manifested by the changes in

the contents of nucleic acids and acidic and basic proteins occur in the shoot apex prior to transition from the vegetative to the reproductive stage of these cultivars.

2.4.7. Surgical experiments :

2.4.7.1. Reproductive parts of monocarpic plants have been reported to be the most important agents which influence the whole plant senescence presumably by drawing metabolites from the vegetative parts (nutrient drain hypothesis) and/or supplying some as yet unknown senescence-inducing factor(s) to the vegetative parts (senescence signal hypothesis). Thus, it has been reported by the majority of the researchers that removal of reproductive parts delays senescence of the whole plant (35,210,257,290,318,339,421), notwithstanding a few reports to the contrary (8,65,137). The present experiments showed that removal of panicle from Rasi and Kalojira rice cultivars, either at the anthesis (0 DAA) or at the grain-filling stage (7 DAA), reduced the loss of chlorophyll and protein over the intact control plants and delayed senescence (Tables 20 & 21). The most interesting feature of panicle removal experiment is that such treatment altered the mode of senescence in Rasi, where the non-sequential mode was changed to the sequential mode, as observed in Kalojira rice and Sonalika wheat cultivars. Although removal of panicle delayed the onset of leaf senescence in Kalojira rice and Sonalika wheat cultivars, there was no change in the mode

of senescence (Tables 21 & 22). It may be noted that the delaying effect due to panicle removal was more pronounced if done at the earlier stages in all the rice and wheat cultivars. This was also true for Rasi. This is imperative because if the sink (panicle) is removed at earlier stages, less nutrients will be drawn out from the source (leaves) and evidently there will be delay in leaf senescence. And this perhaps happened in the present case. Furthermore, if any senescence factor from reproductive parts be involved in initiating senescence, the possibility of its accumulation in leaves would be less if the reproductive sink (panicle) was removed earlier. Another interesting feature of this experiment is that the delaying effect due to panicle removal was more marked in rice compared with that in wheat. One of the possible reasons of such difference may be ascribed to the greater availability of current photosynthate produced by the glumes and awns in wheat than in rice (40,100,185, 356,415), which possibly made it less dependent on source leaf unlike that happened in rice. The evidence in favour of this explanation may be provided from the data presented here, which showed that the initial content of both chlorophyll and protein in glumes was significantly higher in wheat than in rice, but the decline of these components was much greater in wheat than in rice during reproductive development (Figure 29). This suggests that the contribution to grain-filling from the flag leaf of rice was greater than

that of wheat (265) and conversely, the contribution of ear parts to grain-filling was greater in wheat than that in rice (414). It has been suggested by Biswas and Mondal (35) that in wheat the glumes act as intermediaries in the transfer of assimilates from leaves to grains and the contribution of flag leaf is rather indirect. However, the situation appears to be opposite in rice (259). This suggestion could well be applied to the above observations made by us in both rice and wheat.

The analysis of nitrogen and phosphorus contents of the leaves of rice and wheat cultivars from which the panicle was removed at the anthesis (0 DAA) and grain formation (7 DAA) stage showed that their contents decreased relatively slowly in comparison to that of intact control plants with the progress of reproductive development. Interestingly, the removal of panicle after grain-filling stage (14 DAA) neither reduced the loss of nitrogen and phosphorus nor delayed senescence of leaves (Tables 23 to 25), suggesting that the maximal sink demand possibly was developed around the grain-filling stage (14 DAA) causing the greatest depletion of nutrients in leaves and promoting senescence. The delayed removal of panicle produced no effect on the mineral contents of leaves over the intact control plants suggesting that the demand of nutrients from the leaves by the developing grains had already been met by the time the panicle was

removed. The removal of sink has been shown to increase the mineral level in leaves in many species (89,294,443,444). That the rate of senescence could be altered by sink size has also been demonstrated by several workers (72,73,74,75). However, it is also suggested by several workers that drawing of a large amount of metabolites from the vegetative parts by the developing fruits may be an important factor for rapid senescence in many monocarpic plants (32,35,253,258,339). A similar conclusion has been also drawn by Davies and his coworkers working with G2 line of pea (139,182).

The fact that the decline in minerals from leaves, particularly nitrogen and phosphorus, is due to their export to grains could be demonstrated by isotope studies. In fact, [^{32}P]-phosphate isotope experiments revealed that the removal of panicle at the anthesis (0 DAA) or grain-filling stage (7 DAA) significantly increased the retention capacity of [^{32}P]-phosphate of all the three leaves and stem of rice and wheat cultivars (Tables 26 to 28). However, such an act of removal at the later stages of reproductive development (14 and 21 DAA) failed to increase the retention capacity of [^{32}P]-phosphate in the leaves. This suggests that export of major nutrients from the leaves to the grains became relatively insignificant after the grain-filling stage, since the maximal export of [^{32}P]-phosphate took place within 14 DAA after anthesis of rice and wheat cultivars. The isotopic

studies further substantiated the observation that the developing seeds are less dependent on the leaves for the metabolite supply in wheat compared with that in rice. The rise in retention capacity of [^{32}P]-phosphate in leaves and stem of plants from which the panicle was removed at the earlier stages of reproductive development is likely to be due to the absence of sink demand which remained maximal at the earlier stages of reproductive development in intact plants of rice and wheat cultivars.

2.4.7.2. Surgical alterations of the source-sink ratio may provide some interesting clues to the specific involvement of an individual leaf and the reproductive parts in the whole plant senescence of rice and wheat cultivars. Thus, in order to assess this, the plants were first subjected to surgical alteration by defoliation treatment. The senescence behaviour of the remaining leaves was studied after excision of a particular leaf. The results clearly revealed that the removal of the flag leaf had the most significant effect on the enhancement of senescence of the second leaf in all rice and wheat cultivars (Tables 29 to 31). Whereas, removal of the second leaf, although enhanced the senescence of the flag leaf, had less pronounced effect compared with that observed in the second leaf when the flag leaf was removed. The detachment of the third leaf, on the other hand, produced little effect on the senescence of either

the flag or the second leaf. All these results seem to suggest that the flag leaf plays an important role in the mobilization of metabolites to the sink in these cereal cultivars. It is also to be noted that the effect of leaf removal on the senescence of remaining leaves was more pronounced in rice than in wheat. This again suggests that the involvement of leaves in the export of metabolites was less significant in wheat than in rice. These observations are in full agreement with those of Mondal and Choudhuri (258) in rice and Biswas and Mondal in wheat (39). Analysis of leaf nitrogen and phosphorus contents of the remaining leaves as well as [^{32}P]-phosphate retention capacity and export data of the plants from which a particular leaf was excised, lends further credence to the above suggestion (Tables 32 to 37). These data further point out that mobilization of nutrients and metabolites from the leaves to the panicle plays an important role in the senescence development of cereal plants. It was also clear from the results presented above that when the ratio of source to sink was lowered by excision of leaves, particularly the flag or the second, the remaining leaves appeared to compensate the sink demand (312) which remained constant throughout and such a situation presumably enhanced the development of senescence in the remaining leaves due to augmented depletion of metabolites and the resultant exhaustion.

2.4.7.3. As previously stated, the reproductive structures of monocarpic plants may act as a strong sink for drawing nutrients and metabolites from leaves or may send some senescence-inducing stimulus to the leaves or both. In order to further clarify the role of reproductive structures in inducing senescence of rice and wheat cultivars, we attempted to examine the effect of removal of different percentage of spikelets from the panicle or emasculation treatment on the whole plant senescence of rice and wheat cultivars. One of the most interesting features of rice cultivars is that complete removal (100%) of spikelets induced the development of a secondary branch at the axil of the second leaf unlike that in wheat cultivar where no such branch development took place (Table 38 & 39). Furthermore, when the spikelets of the secondary branch of rice was completely removed there was development of the tertiary branch. However, no further branch development occurred when the spikelets of the tertiary branch itself were completely removed. The secondary and tertiary branches contained only two leaves. Removal of different percentage of spikelets from the panicle of the main tiller or emasculation of the panicle in rice and wheat cultivars produced some interesting results. Thus, the removal of 50, 75 and 100 percent spikelets from the panicle or emasculation of the panicle in Rasi and Kalojira rice cultivars caused an induction of secondary branch development while the removal of 25 percent spikelet had no effect on

branch development. Again, the removal of 75 and 100 percent spikelets from the panicle or emasculation of the panicle of the secondary branch was only effective in producing tertiary branch, while the removal of 25 and 50 percent spikelets from the panicle of the secondary branch produced no branch, i.e., this did not induce the tertiary branch development (Tables 38 & 39). Interestingly, even complete removal of spikelets from the tertiary branch or its emasculation treatment failed to produce further branch development (i.e. quaternary branch).

All these results seem, thus, to suggest that the sink size in rice cultivars exerts a regulatory role on the secondary and tertiary branch development. However, the failure of quaternary branch development even after the complete removal of the panicle in the tertiary branch points out that the sink size is not the only limiting factor in inducing branch production. It can be observed from the data of leaf area and seed production capacity of the main-tiller, secondary and tertiary branches that there was a gradual reduction in the number of seeds per panicle and the area of the flag and the second leaf from the main tiller to the tertiary branch (Tables 38 & 39). This leads to the suggestion that a critical balance between the size of the sink and the source was necessary for the induction of branch development in rice cultivars. It appears that such

a balance was lost in the tertiary branch and hence no further branch development occurred at the leaf axil of this branch. These interesting results however need further critical evaluation.

It is clear from the above results that the reproductive parts (panicle) exerted an inhibitory influence on side branch development in rice plants comparable with the phenomenon of 'apical dominance'. Nevertheless, the complete inhibition of development of quaternary branch from the tertiary branch clearly indicates that some factor(s), associated with branch development, became limiting in the tertiary branch. As a consequence of this, there was no quaternary branch development and the above-ground parts of the plant completely senesced and died along with the tertiary branch. It is tempting to speculate that the apical dominance-like effect, as exerted by the panicle, appears to regulate the onset of whole plant senescence. Thus, the removal of a higher percentage of spikelets was necessary for destroying the apical dominance-like effect and inducing the development of tertiary branch than what was necessary for the induction of secondary branch development in both the rice cultivars studied.

Another factor which seems to be involved in this phenomenon is the leaf area. The seed production capacity of different branches was found to be directly related with the leaf area, since leaf is the main source for supplying photosynthate and other metabolites for the seed development (44, 232). It seems, therefore, that the initiation of side branches in rice cultivars was the consequence of a balance

between the inhibitory influence of the panicle and the promotive influence of the leaf subtending the branch, possibly mediated by metabolites and phytohormones. Evidently, the failure of quaternary branch development at the second leaf axil of the tertiary branch even after complete removal of spikelets or emasculation treatment seems to point out that the branch initiation factor(s), possibly supplied by the second leaf of tertiary branch, became limiting due to the reduction of leaf area below a critical level. That the leaf provides an essential factor(s) for the side branch development can be further corroborated from the findings that complete removal of both spikelets and the second leaf from the main tiller and similar treatment of the secondary branch in both rice cultivars completely failed to induce secondary and tertiary branch development, respectively. It is to be noted here that the removal of spikelets from the main tiller of the wheat cultivar did not initiate secondary branch development, suggesting that inhibitory influence of the panicle is species specific. However, there may be another possible reason for such difference observed in rice and wheat cultivars. In rice, the grain-filling is largely dependent on the supply of photosynthate and metabolites from leaves, whereas in wheat the reproductive parts also actively participate in the grain-filling process, where the leaves often play a secondary role. Thus, the removal of total sink in wheat cultivar

possibly did not cause sufficient alteration in the cellular metabolites in the second leaf which seems necessary for branch development. A recent report by Bangerth (14) shows that polar transport of IAA from the earlier developing seeds inhibits the development of other seeds and also observed a Primigenic dominance (PP), a kind of correlative inhibition, in which the earlier developing seeds inhibits later developing organs. Such transport of IAA from the fruits has also been found to be closely related to the number of seeds present (385) which inhibits lateral bud formation. It has also been suggested by several authors that cytokinins originating from roots possibly inhibit IAA metabolism and promote lateral bud growth (154,325). The application of cytokinin or IAA and a combination of both in lanoline paste on the cut surface of the depanicked plants had no influence on secondary branch development as noted in the present study (data not shown). This suggests that the apical dominance like influence of the panicle may be exerted through some substance(s) other than IAA and/or cytokinins. Admittedly, this can not be said with certainty unless labelled IAA or cytokinins are used in such experiments.

Looking at the senescence behaviour of leaves of two rice and one wheat cultivars after removal of different percentage of spikelets from the panicle or emasculation treatment, one can easily infer that senescence was delayed

in both rice and wheat cultivars due to removal of spikelets or emasculation treatment and the delaying effect gradually increased with increasing removal of spikelets (Tables 40 to 42). Thus, the reduction of sink demand was related to the progress of senescence, although complete removal of the panicle (sink demand) did not prevent senescence completely. This observation finds support from the observations of Biswas and Mondal (39) in wheat, Valio and Polo (421) in bean, Crafts-Brandner and Egli (73) in soybean and Kelly and Davies (182) in G2 pea. Another interesting feature of the present study is that a minimum of 50 percent spikelet removal from the main tiller was necessary to induce secondary branch development at the second leaf axil of the main tiller of Rasi cultivar as well as for inducing a change from the non-sequential to the sequential mode of senescence. To achieve such results in the secondary branch of Rasi, a minimum of 75 percent spikelet removal was necessary. Although there was a delaying of senescence of leaves in Kalojira due to spikelet removal or emasculation treatment, the sequential pattern of senescence is maintained throughout the reproductive development.

If one follows the pattern of leaf senescence of secondary and tertiary branches, it will be seen that they always showed sequential and non-sequential mode according to the mode shown by the main tiller unless, of course the

spikelets were removed, suggesting that a particular mode of senescence is genetically controlled. Although the removal of 75 and 100 percent spikelets or emasculation of tertiary branch delayed leaf senescence, quaternary branch was not formed in either rice cultivar and consequently the mode of leaf senescence behaviour in Rasi was not changed in this branch, i.e., it remained non-sequential like the main tiller (Table 45) because there was no alternative sink at the second leaf axil of the tertiary branch.

It is noteworthy that the total longevity of the main tiller (i.e. the whole plant) was extended by about 42 days over the unexcised control plants owing to side branch production at the second leaf axil. Hence it may be concluded that both leaves and reproductive parts might exert regulatory role in side branch production, which, in turn, might control the longevity of the whole plant. The senescence inducing substance, if formed in the subtending second leaf, was not transmitted to the leaves of the side branch. Had this happened, the second leaf of Rasi would have then senesced earlier than the flag leaf of the side branch which was, however, not the case. Thus, in rice, the failure of further branch production on removal of spikelets marks the end of the whole plant.

C O N C L U S I O N

It was observed in the present investigation that among the rice cultivars studied, Rasi and Sashyasri showed a non-sequential mode of leaf senescence, whilst Kalojira and Badsabhog showed a sequential mode of leaf senescence. The other two rice cultivars, Patnai and Kalma, showed an intermediate type. Both the wheat cultivars (Sonalika and Kalyansona), however, showed a sequential mode of senescence. Conceivably, had the senescence factor come from the reproductive parts (seeds), the flag leaf would have always senesced first, regardless of cultivars due to its closest proximity to the reproductive parts. But this was not the case, since some rice cultivars showed non-sequential mode of senescence. Recent observations of Davies and his co-workers in G2 pea on the quantitative export from the fruit to the apex and the identification of exported materials as sucrose and malic acid, which are ineffective as senescence inducing substances, led them to abandon the concept of senescence signal hypothesis (139,182).

There was a distinct correlation between leaf senescence behaviour with xylem parameters at the juncture of

leaf lamina and leaf sheath in different rice and wheat cultivars, suggesting that conducting vessels and the orthostichous connections between leaves and reproductive parts play an important role in nutrient withdrawal process from leaves to the reproductive parts, and also hormones, mineral nutrients and water from roots to the shoot, thereby determining senescence behaviour of the leaf. In wheat, the pattern of leaf senescence appears to be less dependent on metabolite supply from leaves, unlike rice, since the reproductive parts of wheat themselves provide an appreciable amount of assimilates to the growing seeds which are, therefore, less dependent on the source leaf for their nourishment. The period of maximal export of nutrients in rice and wheat was generally found to be prior to grain maturation stage when maximal nutrient stress in the leaves presumably developed as indicated by the largest proline accumulation. Such a situation resulted in a great hormonal disbalance favouring senescence development, i.e. depletion of senescence retarding hormones, such as cytokinins (and possibly GA_3), and accumulation of senescence promoting hormones, such as ABA and ethylene.

Surgical removal of panicle (sink) or emasculation treatment of the panicle at the early stages of reproductive development, although delayed senescence by several days, could not prevent it in both rice and wheat cultivars and

all these cultivars showed a uniform pattern of sequential leaf senescence possibly due to development of an alternative sink in the form of a secondary or a tertiary branch. Similarly, external application of senescence retarding or promoting hormones delayed or enhanced the senescence process for a few days without altering the leaf senescence behaviour, but failed to prevent senescence indefinitely in both rice and wheat cultivars. In desinked rice cultivars, a secondary branch developed at the second leaf-axil which also produced a tertiary branch, if further desinked at the earlier stages of reproductive development. Interestingly, the mode of leaf senescence of 'daughter' branch was exactly the same as that of the 'mother' plant from which it developed, suggesting that the pattern of leaf-senescence exhibited by each cultivar is an inherent and genetically controlled character of a species or cultivar. Apparently, the above results seem to suggest that nutrient withdrawal might not be the sole factor in inducing the whole plant senescence, but, no doubt, this was a major senescence accelerating factor in these cereal cultivars. While in rice, it could be interpreted as due to the development of a secondary branch at the leaf axil as an alternative sink and hence the nutrient export from the 'mother' plant to the 'daughter' branch remained unabated, it could not, however, be explained in wheat cultivars where there was no development of an alternative sink in the form of a secondary branch. One of the reasons of the failure of

secondary branch development in wheat plants might be speculated as due to their leaf area becoming limiting and also due to their less storage ability resulting perhaps from less involvement of the leaves in metabolite supply to the developing seeds. In wheat, the stored metabolite level in the leaves might play a critical role in inducing branch development. Furthermore, according to Kelly and Davies (182) shifting in nutrient partitioning occurs during flowering when the leaves become committed to the supply of nutrients and metabolites only to the reproductive parts, depriving the other vegetative parts including roots, and thereby hastening the senescence process of the vegetative parts.

One of the most interesting features of rice cultivar is that the longevity of the whole plant could be increased up to the senescence of tertiary branch (by about 42 days). As there was no further development of quaternary branch the longevity could not be further extended. The failure of the tertiary branch to develop quaternary branch might be attributed to the extreme reduction of leaf area in this branch. It must be pointed out that the second leaf of the 'mother' branch from which the alternative sink in the form of a secondary or a tertiary branch developed always senesced earlier, possibly due to development of a nutrient exhaustion stress resulting from the metabolite supply to

the 'daughter' branch. Another point of interest is that if any senescence factor(s) was presumably produced within the leaves during floral differentiation (when maximal increase in genetic materials such as DNA, RNA and total protein took place in the shoot apex), it was certainly not transmitted to the 'daughter' branch. Had this happened, the 'daughter' branch would have senesced much earlier than what was observed in rice cultivars. It is also to be noted that senescence of photoperiod-sensitive rice cultivars, such as Kalojira, Badsabhog, Patnai and Kalma (Table 48), could be enhanced substantially (about six months) if grown in the field under unfavourable photoperiodic conditions. A number of reports showed that the senescence of monocarpic plants could be prevented almost indefinitely if the flowering could be prevented by subjecting the plants to unfavourable conditions (64,77,307,432).

If all these facts are taken together, there seems to be no other alternative but to conclude that the genes responsible for inducing senescence are perhaps expressed in the leaf at the time of flowering itself in monocarpic plants. The male hemp plant (Cannabis sativa L.), without fruits, senesced almost at the same time as the female plant bearing fruits. This was also true in spinach (Spinacea oleracea). Thus, in these plants flowering and not the fruiting is the main criterion for inducing senescence of the whole plant.

Furthermore, it was also reported by Kulkarni and Schwabe (193) that senescence factor might be produced in the leaves of Kleinia articulata. And this might also happen in cereal species. Nevertheless, the ultimate manifestation of senescence syndrome may differ somewhat in different species. Sabater (351) has suggested that the transition from a hormonal equilibrium retarding senescence to another equilibrium accelerating senescence may be triggered by genes, including a marked change in the supply or in the synthesis of an individual hormone. Nonetheless, the exact mechanism of expression and the location of the gene(s) remained to be explored and a great deal of further work at the molecular level is needed to resolve the problems pertaining to this programmed self-destructive process of monocarpic plants.

S U M M A R Y

The mechanism of monocarpic senescence has been dealt with at length as would be evident from the overwhelming number of research publications. Nonetheless, the exact mechanism of monocarpic senescence is not clearly understood as yet. The present investigation aims at analysing the possible mechanism of monocarpic senescence employing different cultivars of rice (Oryza sativa L) and wheat (Triticum aestivum L), viz. short-statured, photoperiod-insensitive rice cultivars - Rasi and Sashyasri; medium-statured, photoperiod-sensitive cultivars - Kalojira and Badsabhog; tall-statured, photoperiod-sensitive cultivars - Patnai and Kalma; and wheat cultivars - Sonalika and Kalyansona.

The patterns of leaf senescence in all these cultivars were studied in order to get an insight into the correlative control and possible cause of monocarpic senescence in rice and wheat plants. To analyse the cause of different patterns of senescence in these cultivars, and to explore the possible role of mobilization of metabolites from leaves in the development of these senescence patterns, some physiological,

biochemical, anatomical and hormonal studies were carried out in intact as well as surgically altered cultivars of rice and wheat. The study was conducted during the progress of reproductive development of these cereals passing through different stages, such as anthesis (0 day after anthesis or 0 DAA), grain-filling (7 DAA), grain development (14 DAA), grain maturation (21 DAA) and senescent stage (28 DAA). In most of the studies the decline in chlorophyll and protein was taken as indicators of senescence development. The important findings are summarised below.

The data of the levels of chlorophyll and protein and the percentage of yellowing patches in the flag, second and third leaf revealed that short-statured Rasi and Sashyasri rice cultivars displayed a non-sequential mode of leaf senescence behaviour where the youngest flag leaf senesced earlier than the ontogenetically older second leaf. On the other hand, the medium-statured Kalojira and Badsabhog rice and Sonalika and Kalyansona wheat cultivars showed a sequential mode of leaf senescence behaviour where the leaves senesced strictly according to their chronological age. However, the tall-statured Patnai and Kalma rice cultivars could be placed in between sequential and non-sequential mode of leaf senescence (intermediate type) where both the flag and second leaf senesced almost simultaneously.

The data of the loss of nitrogen and phosphorus, the two most mobile elements in plants, from the three uppermost leaves of these cereal cultivars revealed that it was strictly according to the mode of senescence as displayed by each of the above cultivars. The data of mobilization of [^{32}P]-phosphate from leaves to the grains and its retention capacity by the fed-leaf revealed that the export pattern of this isotope varied among species and cultivars. However, the export of [^{32}P]-phosphate to the grains was always higher in rice than that in wheat. In rice cultivars, the export of this isotope from the leaves was directly proportional to the sink strength (panicle weight) which was greater in the tall-statured cultivar. The export of [^{32}P]-phosphate from leaves to the grains gradually increased, reaching the maximal point at the grain development stage (14 DAA), declining thereafter. When calculated on per unit leaf area basis, the maximal export of [^{32}P]-phosphate was found to take place from the flag leaf of Rasi. In Kalojira and Patnai the difference in the export of radioisotope from the flag and the second leaf was not so significant. The data also revealed that the export of [^{32}P]-phosphate was inversely proportional to the leaf area. Thus, the maximal export took place from Rasi cultivar with maximal leaf senescence and minimal export took place in Patnai with maximal leaf area. The export pattern of radiophosphate from Sonalika wheat was similar to that of Kalojira rice

cultivar. In general, the retention capacity of [^{32}P]-phosphate decreased gradually with progress of reproductive development in both rice and wheat cultivars. The retention capacity of labelled phosphate followed the same trend as that of leaf senescence in both rice and wheat cultivars. When the isotope was fed through the roots and measured in the leaves and seeds, it was observed that the transport of [^{32}P]-phosphate gradually decreased with the progress of reproductive development in all the cultivars. The extent of transport of labelled phosphate was always greater in rice than in wheat. The export of [^{32}P]-phosphate was again proportional to the senescing condition of the leaf, i.e. the more was the leaf approaching senescence, the lesser was the export of radiophosphate from the roots.

Analysis of the xylem parameters at the juncture of leaf lamina and leaf sheath as well as the data of leaf area indicated a clear correlation between these parameters and the pattern of leaf senescence. Thus, in the non-sequential Rasi rice cultivar, the leaf area and xylem parameters, such as the number of vascular bundles at the juncture of leaf lamina and leaf sheath, the area of xylem vessels in a bundle and the area of lumen of the largest vessel, were approximately double in the second leaf than in the flag. In the sequential Kalojira rice cultivar, such parameters were almost equal in both flag and second leaf, whereas

in the intermediate Patnai rice and Sonalika wheat cultivars, these were marginally greater in the second than in the flag leaf.

External application of BA (benzyladenine, 4.4×10^{-4} M), GA₃ (gibberellic acid, 2.9×10^{-4} M) and their combination (BA + GA₃) significantly delayed leaf senescence, the effect being most pronounced with (BA + GA₃), followed by separate application of BA and GA₃. However, such treatments did not alter the mode of senescence displayed by each cultivar. ABA (abscisic acid, 7.5×10^{-5} M), on the other hand, promoted leaf senescence in all the cultivars and also did not alter the mode of leaf senescence. The loss of nitrogen and phosphorus from the leaves of rice and wheat cultivars was inhibited by BA, GA₃ and (BA + GA₃) treatment but it was promoted further by ABA treatment. BA treatment also enhanced retention capacity of [³²P]-phosphate of the fed leaf and also the export from leaves to grains in all the cereal cultivars, whereas ABA acted in an opposite manner. Although BA enhanced the export of [³²P]-phosphate, it delayed senescence. Whereas ABA decreased [³²P]-phosphate export but promoted senescence.

An analysis of the changes in histone protein and RNA in leaves of rice and wheat cultivars revealed that with the approach of senescence there was a decline in RNA and rise in histone protein. And there was also a consistent

decline in RNA:histone ratio. While BA increased RNA synthesis, raised RNA:histone ratio and decreased histone protein, ABA decreased RNA, lowered RNA:histone ratio and increased histone protein in all the leaves of cereal cultivars with ageing and senescence.

Concomitant with the decrease in protein level, there was a rise in protease activity and free amino acid accumulation in the leaves which were proportional to the ageing and senescing condition of the leaf. Treatments with BA and ABA produced an inhibitory and promotive effects, respectively, on these parameters.

There was a senescence-related proportional increase in malondialdehyde (MDA) content, (which is an oxidation product of polyunsaturated membrane fatty acids and a reliable indicator of membrane deterioration) in leaves of different rice and wheat cultivars suggesting that the loss of membrane integrity is a function of ageing and senescence in these cultivars. That such membrane deterioration is induced by free radicals could be indirectly substantiated from the observations of the decline in the activities of superoxide dismutase (SOD) and catalase in leaves with approaching senescence, and such a decline possibly favoured free radical accumulation and induced membrane deterioration. The rise in peroxidase activity during senescence of leaves of these cultivars might also

facilitate oxidative degradation of cellular macromolecules. The accumulation of MDA and changes in free radical scavenging enzymes were proportional with ageing in rice and wheat cultivars. External application of BA significantly retarded MDA accumulation and increased SOD, catalase and peroxidase activities. ABA application, on the contrary, produced an opposite effect.

The rate of transpiration either by the whole plant or by an individual leaf, generally taken as an indicator of stomatal opening and closing as well as capacity for uptake of cytokinins, nutrients and water from roots to aerial parts, gradually decreased during the reproductive development of rice and wheat cultivars with the concomitant increase in proline accumulation. In Rasi, the decline in the rate of transpiration and rise in the accumulation of proline were greater in the flag leaf than in the second leaf at the senescent stage; whereas in Kalojira rice and Sonalika wheat cultivars the sequence of these events occurred according to the chronological age of the leaf. Foliar application of BA enhanced transpiration rate and also suppressed proline accumulation, whilst ABA application gave an opposite effect.

In order to assess the role played by senescence retarding and promoting hormones in whole plant senescence, the endogenous levels of cytokinin-like (CK-like) substances

and ABA and the release of ethylene from the leaves were measured with the progress of reproductive development of rice and wheat cultivars. The CK-like substances and the ratio between CK-like substances and ABA gradually decreased, while ABA and ethylene increased with the progress of reproductive development. The level of CK-like substances was in general higher in rice than in wheat. In the Rasi rice cultivar, CK-like substances and the ratio between CK-like substances and ABA was greater in the second leaf than in the flag leaf at the senescent stage. An opposite trend was noticed in Kalojira rice and Sonalika wheat cultivars. The level of ABA gradually increased in all the leaves of rice and wheat cultivars, reaching the maximal level at the grain maturation stage (21 DAA), declining thereafter. The release of endogenous ethylene was higher in the flag and second leaf at the anthesis stage (0 DAA), followed by a decline up to the grain development stage (14 DAA) and a rise thereafter.

There was an increase in the content of total protein and nucleic acids in the shoot apex 9-12 days before panicle emergence in all the cereal cultivars studied. After that, there was a decline in the content of these macromolecules, with the concomitant rise in the content of histone protein. These results indicated that marked changes in the genetic materials, as manifested by the changes in nucleic acids

and both acidic and basic proteins, occurred in the shoot apex of these cereal cultivars prior to transition from the vegetative to the reproductive stage.

Reproductive parts of monocarpic plants are important agents which influence the whole plant senescence presumably by drawing metabolites from the vegetative parts and/or supplying some yet unknown senescence factor(s) to the vegetative parts. The present experiment showed that the removal of panicle at the anthesis (0 DAA) and grain-filling stages (7 DAA) markedly delayed the leaf senescence of all cultivars studied. Such treatments also altered the mode of leaf senescence from non-sequential to sequential in only Rasi rice cultivar possibly due to development of an alternative sink at the second leaf axil. Although such treatment delayed senescence in wheat cultivar, the effect was much less pronounced compared with that of rice cultivars. The extent of senescence delaying effect diminished as the act of surgical removal of the panicle was delayed. Thus, such treatments at the grain development (14 DAA) and grain maturation (21 DAA) stages had no effect on the retardation of leaf senescence and could not alter the mode of leaf senescence even in Rasi as there was no development of alternative sink. The delaying effect due to panicle removal was greater in rice than in wheat. One of the possible reasons of such difference might be ascribed to greater

availability of current photosynthate produced by the glumes in wheat than in rice, making the former less dependent on the source leaf unlike that in rice. Thus the content of chlorophyll and protein of glumes was significantly higher in wheat than in rice at the earlier stages, while the decline was greater in wheat than in rice during the later stages of reproductive development.

The analysis of nitrogen and phosphorus contents of the leaves of rice and wheat cultivars from which the panicle was removed at the anthesis (0 DAA) and the grain-filling (7 DAA) stages showed that their contents decreased relatively slowly as compared with that of the intact control plants with the progress of reproductive development. The removal of panicle at the grain development (14 DAA) stage could neither reduce the loss of nitrogen and phosphorus nor delay the senescence suggesting that the maximal sink demand possibly was developed around the grain development stage (14 DAA) which caused the greatest depletion of nutrients and subsequently enhanced senescence. When the panicle was removed at the grain development stage (14 DAA) or at the later stages, there was no change in the mineral contents as well as senescence of the leaves over the intact control plants. The study with [^{32}P]-phosphate export from leaves also corroborated this.

The surgical excision of the flag leaf had the most significant effect on the enhancement of senescence in all the rice and wheat cultivars. While removal of the second leaf also enhanced the senescence of the flag leaf, the extent was less prominent compared with that of the second leaf when the flag leaf was removed. The removal of the third leaf had little effect on the senescence of the other two leaves. These results suggested that the flag leaf played an important role in the mobilization of metabolites in the cereal cultivars. Analysis of leaf nitrogen and phosphorus contents of the remaining leaves as well as [^{32}P]-phosphate retention capacity and export data of rice and wheat cultivars from which a particular leaf was excised provided further credence to the above suggestion.

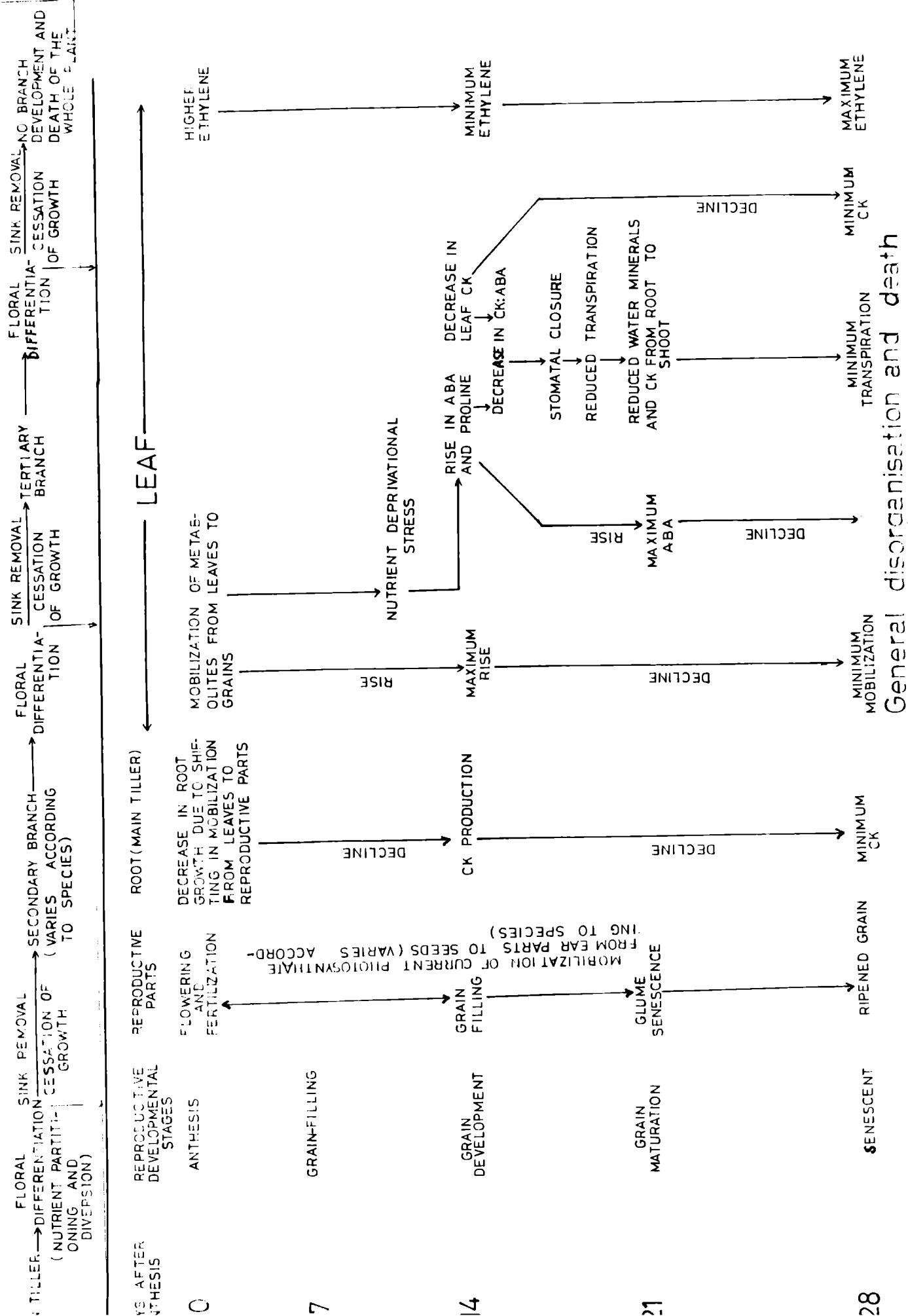
In order to further clarify the role played by the reproductive structures on the senescence process of rice and wheat cultivars, attempts were made to examine the effects of removal of different percentage of spikelets from the panicle or emasculation treatment of the panicle on the whole plant senescence. The removal of 50, 75 and 100 percent spikelets from the panicle or emasculation treatment in the main-tiller of rice cultivars induced the development of secondary branch with two leaves at the axil of the second leaf. Similarly, removal of 75 and 100 percent spikelets from the panicle of the secondary

branch of rice or the emasculation treatment induced the development of tertiary branch from its second leaf axil. But such treatment on the tertiary branch could not induce further branch development in both the rice cultivars. Interestingly, such surgical treatment on wheat plant had no effect on branch development. The leaf area of the flag and the second leaf of the main-tiller, secondary branch and tertiary branch gradually decreased with the concomitant decrease in seed number.

The removal of 50, 75 and 100 percent spikelets from the panicle of the main tiller or its emasculation treatment delayed leaf senescence in both rice and wheat cultivars and altered the non-sequential mode of senescence to sequential mode in Rasi rice cultivar. However, the delaying effect of spikelet removal on senescence was greater in rice than in wheat. Similarly, 75 and 100 percent spikelet removal or emasculation treatment of the secondary branch of rice cultivars delayed leaf senescence but altered the mode of senescence only in Rasi. However, 25 and 50 percent removal of spikelets had no effect on either branch development or delaying of senescence of the secondary branch. Such treatment on tertiary branch, although delayed leaf senescence, did not alter the mode of leaf senescence in Rasi possibly due to the absence of an alternative sink in the form of a quaternary branch. It is noteworthy that

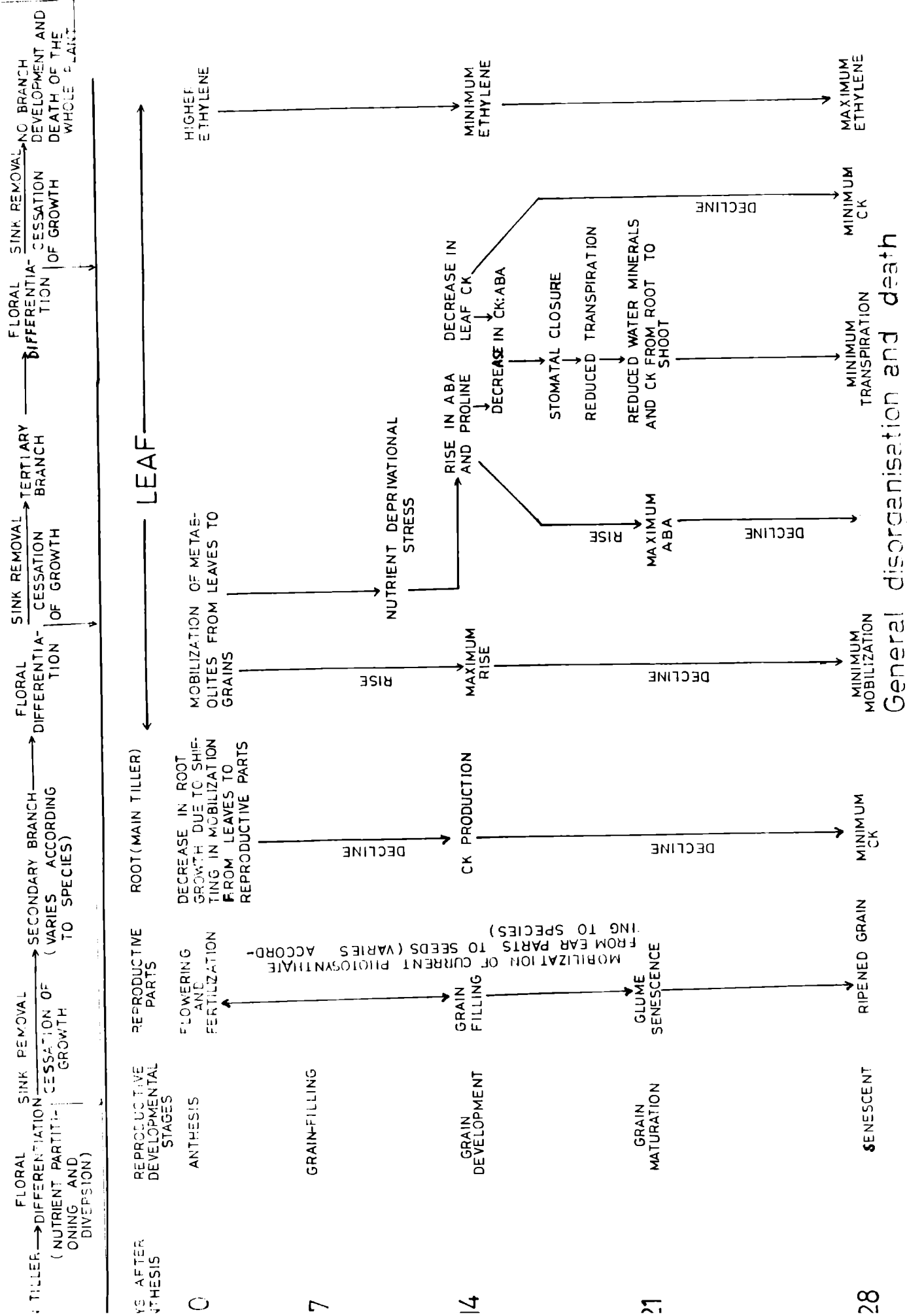
the total longevity of the main-tiller of rice (whole plant) could be extended by continuous allowance of branch development over the untreated intact control plants. Thus, in rice the failure of further branch production (quaternary) due to removal of spikelets or emasculation treatment of the tertiary branch marked the end of the whole plant longevity.

EVENTS OF MONOCARPIC SENESCENCE IN CEREALS



FIGURES

EVENTS OF MONOCARPIC SENESCENCE IN CEREALS



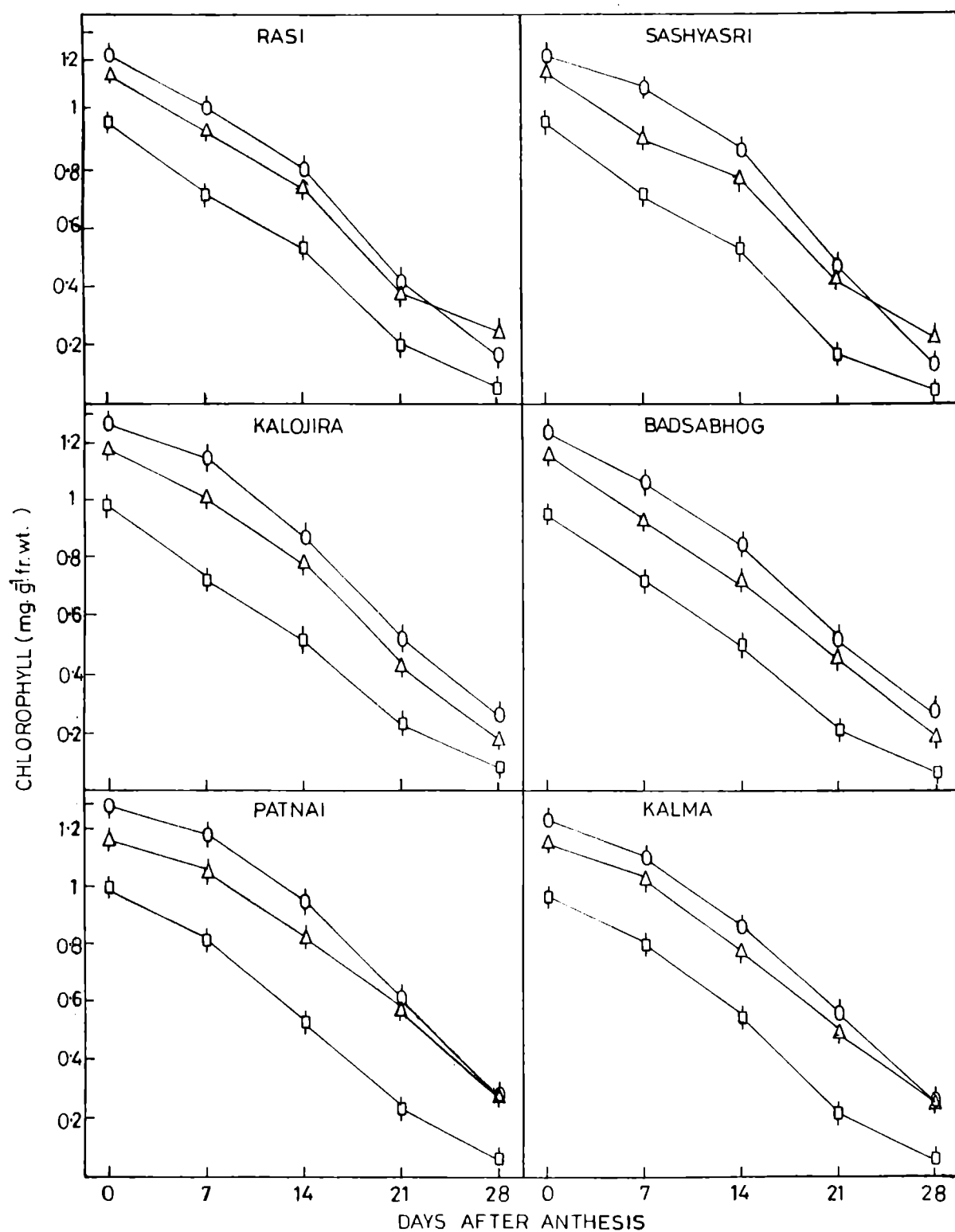


Fig.1. Changes in chlorophyll content in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of six rice cultivars during the progress of reproductive development. Data were recorded at intervals of 7 days from anthesis to senescent stage of each rice cultivar. Bars indicate \pm SE for six replicates.

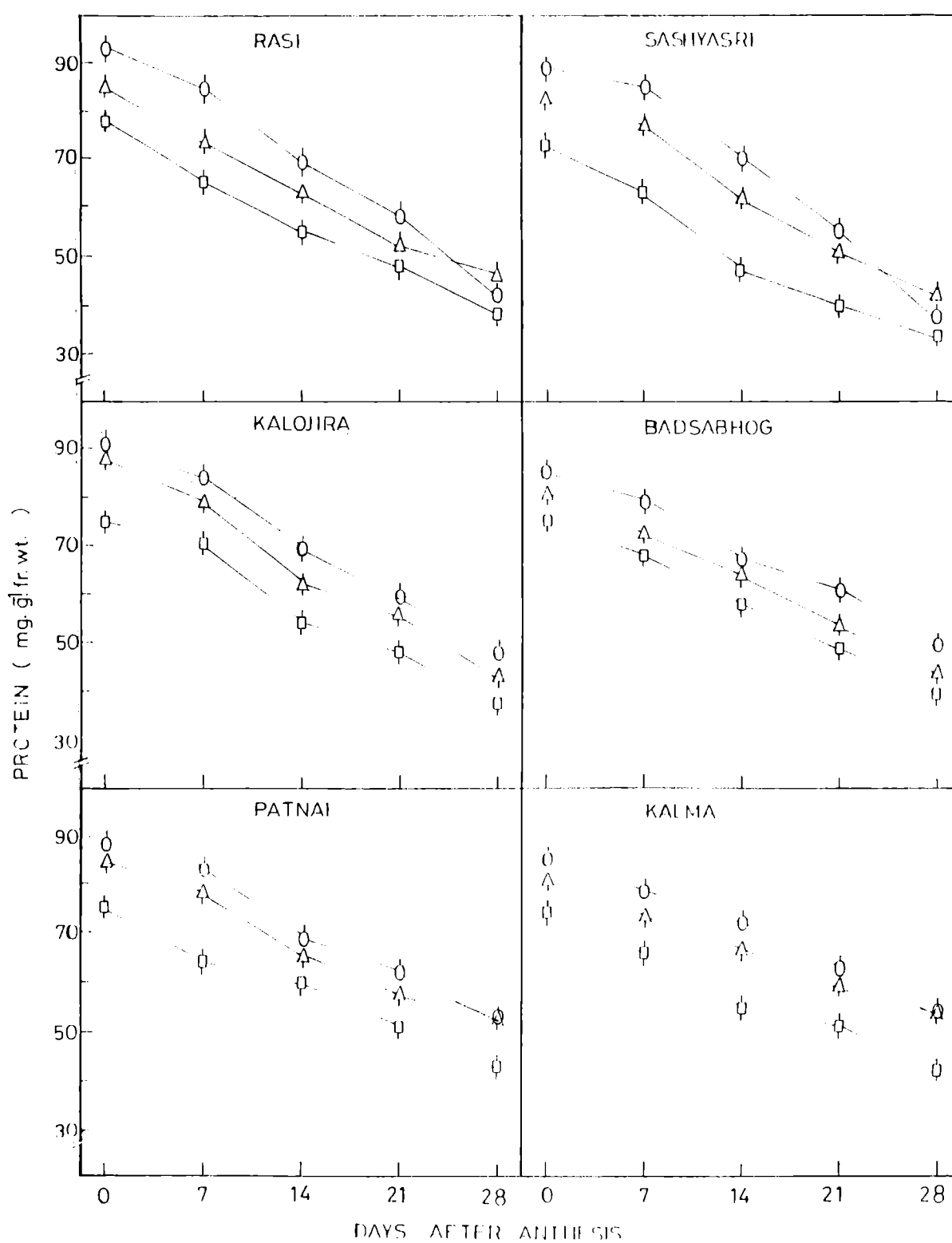


Fig.2. Changes in protein content in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of six rice cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

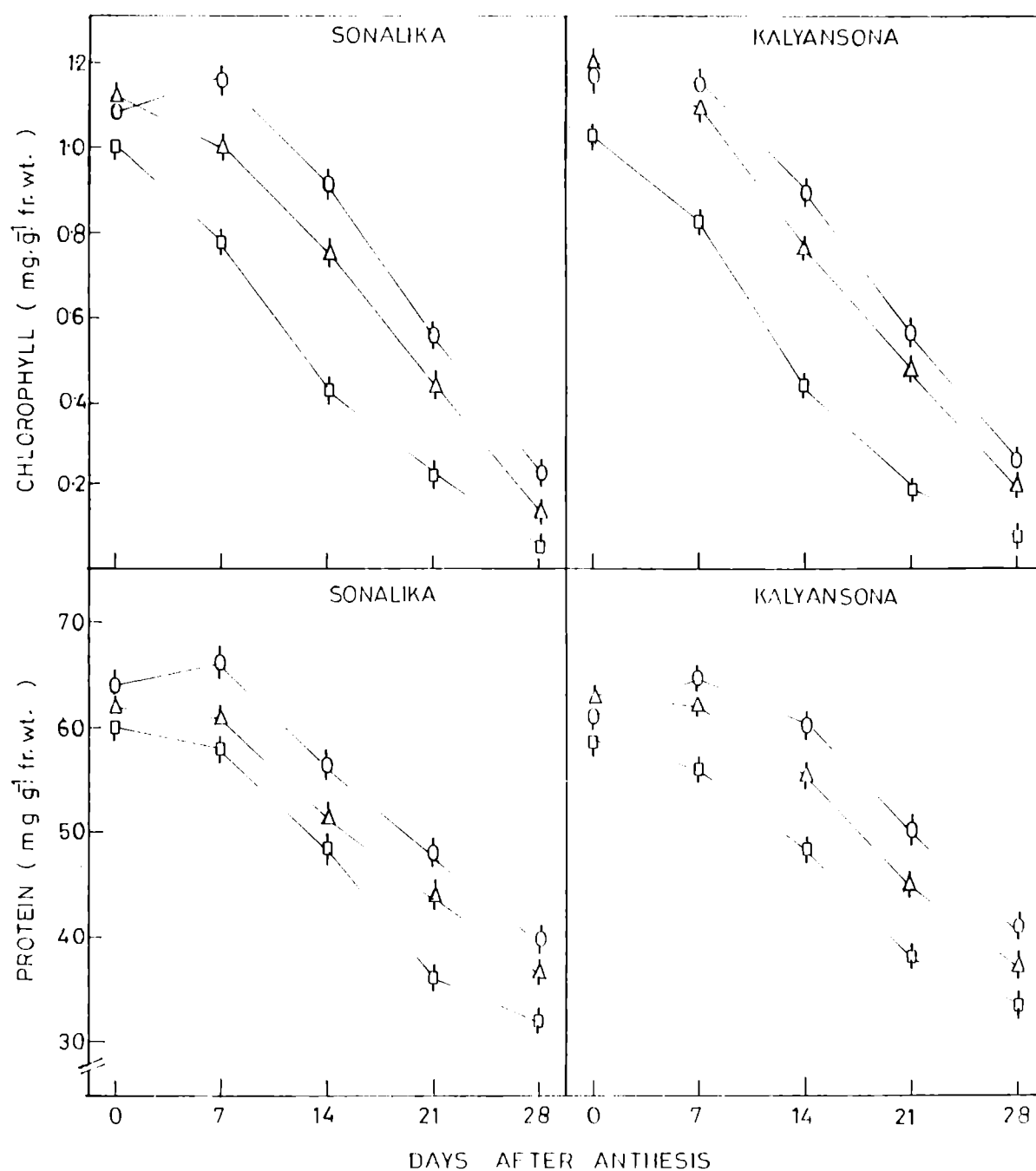


Fig.3. Changes in chlorophyll and protein contents in the flag (○—○), second (△—△) and third (□—□) leaf of two wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

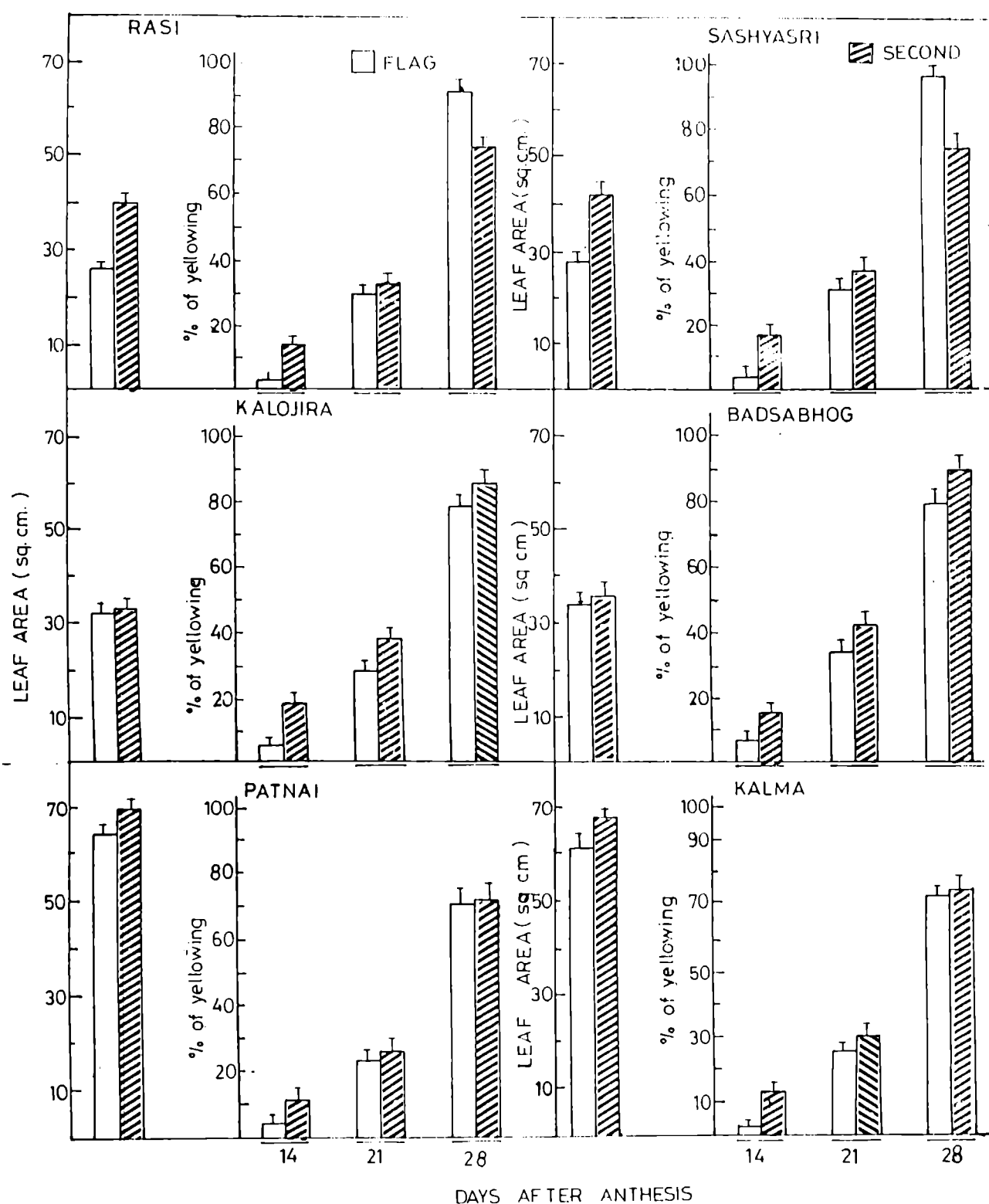


Fig.4. Total leaf area and changes in the percentage of yellowing patches (expressed as percentage of total leaf area) in the flag (□) and second (▨) leaf of six rice cultivars. Data were recorded as in Fig.1. Bars as in Fig.1.

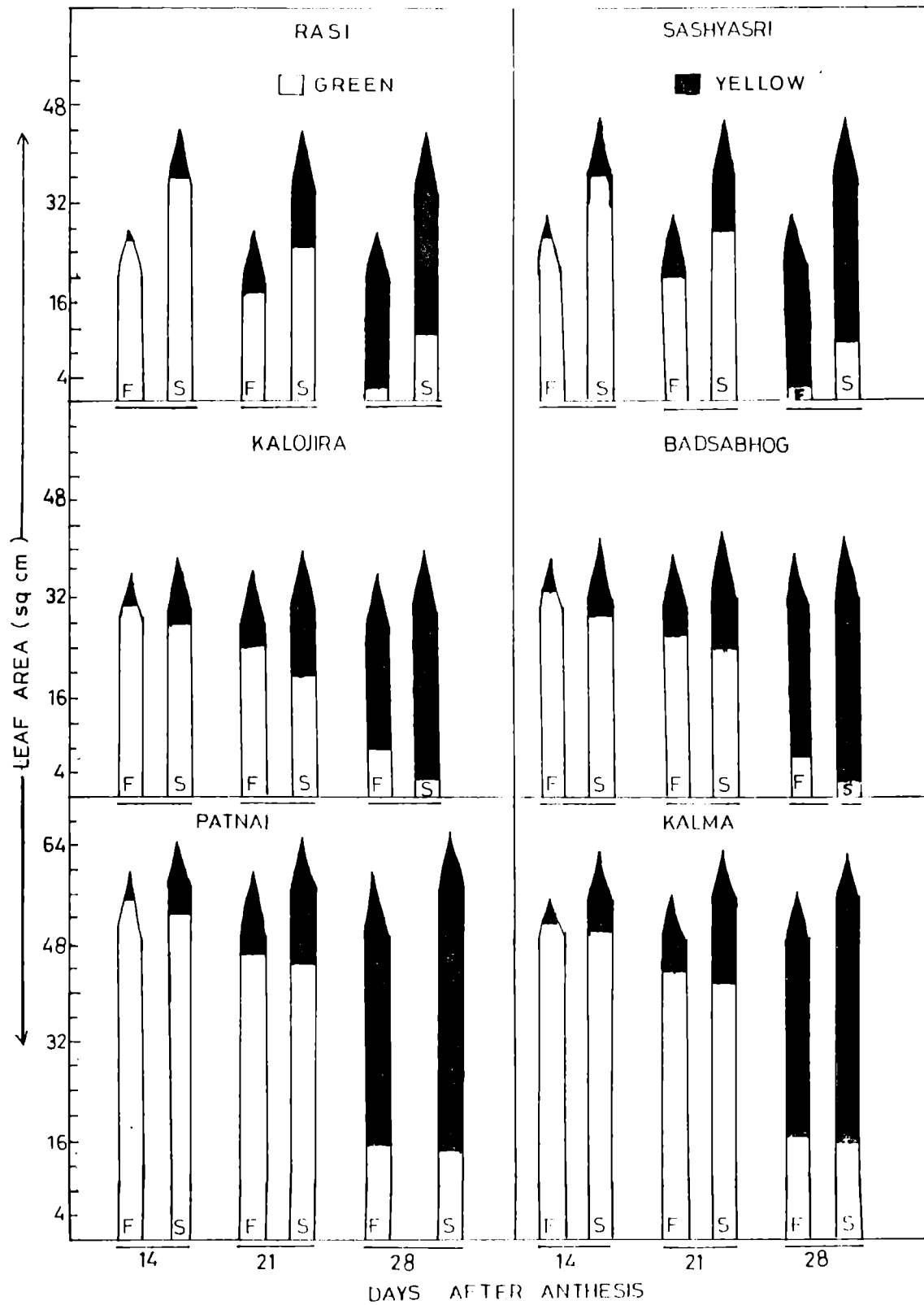


Fig.5. Diagrammatic representation of green (□) and yellow (■) area of the flag (F) and second (S) leaf of six rice cultivars during the progress of reproductive development.

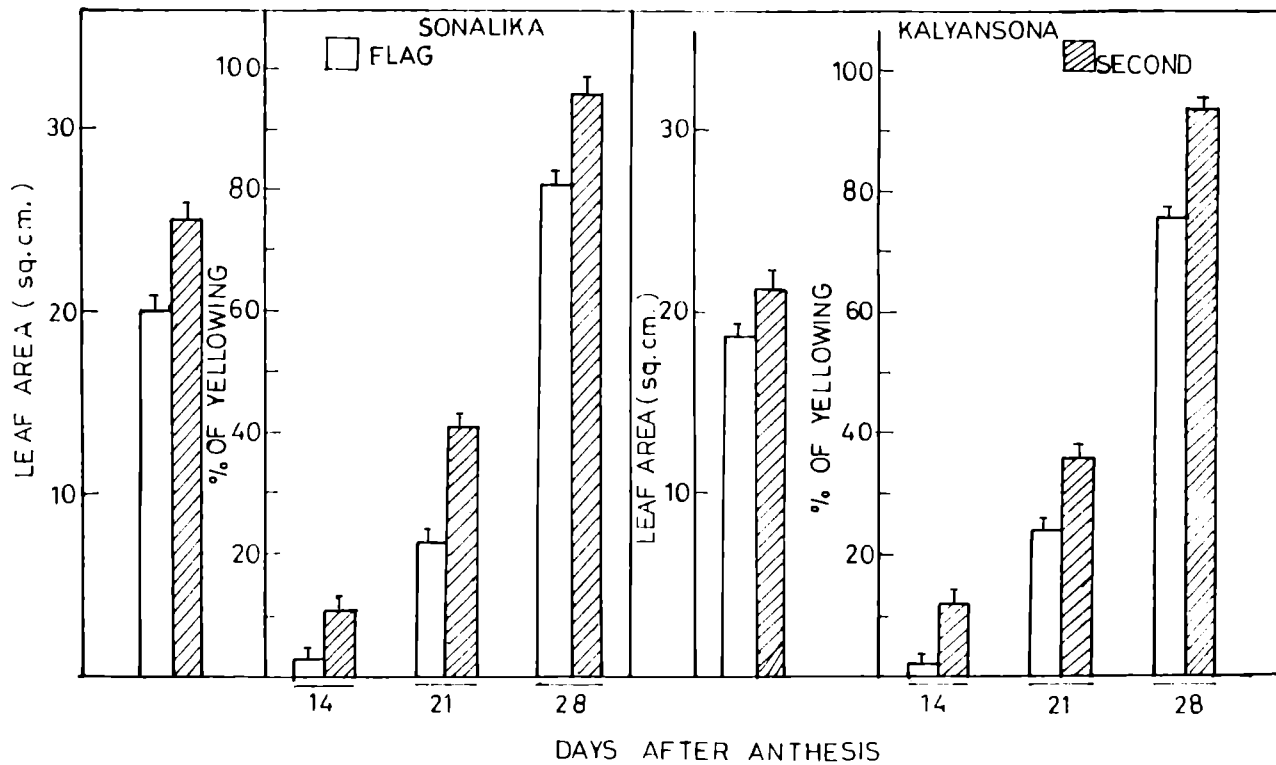


Fig.6. Total leaf area and changes in the percentage of yellowing patches (expressed as percentage of total leaf area) in the flag (□) and second (▨) leaf of two wheat cultivars. Data were recorded at intervals of 7 days from grain development to senescent stage of each cultivar. Bars as in Fig.1.

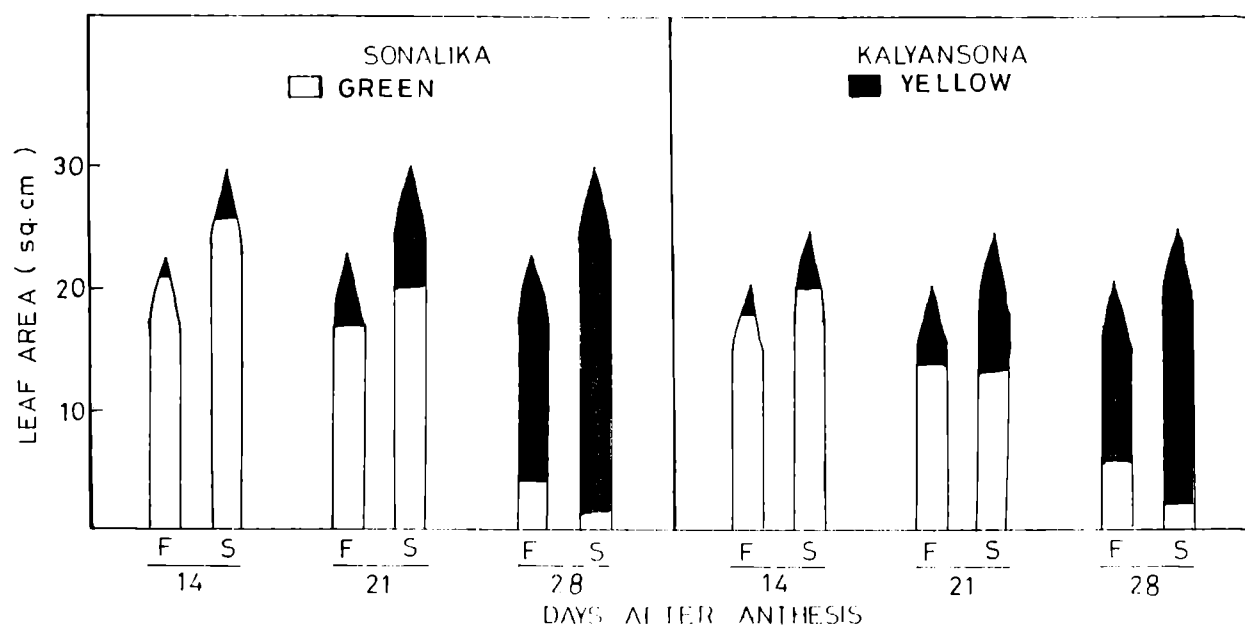


Fig.7. Diagrammatic representation of green (□) and yellow (■) areas of flag (F) and second (S) leaf of two wheat cultivars during the progress of reproductive development.

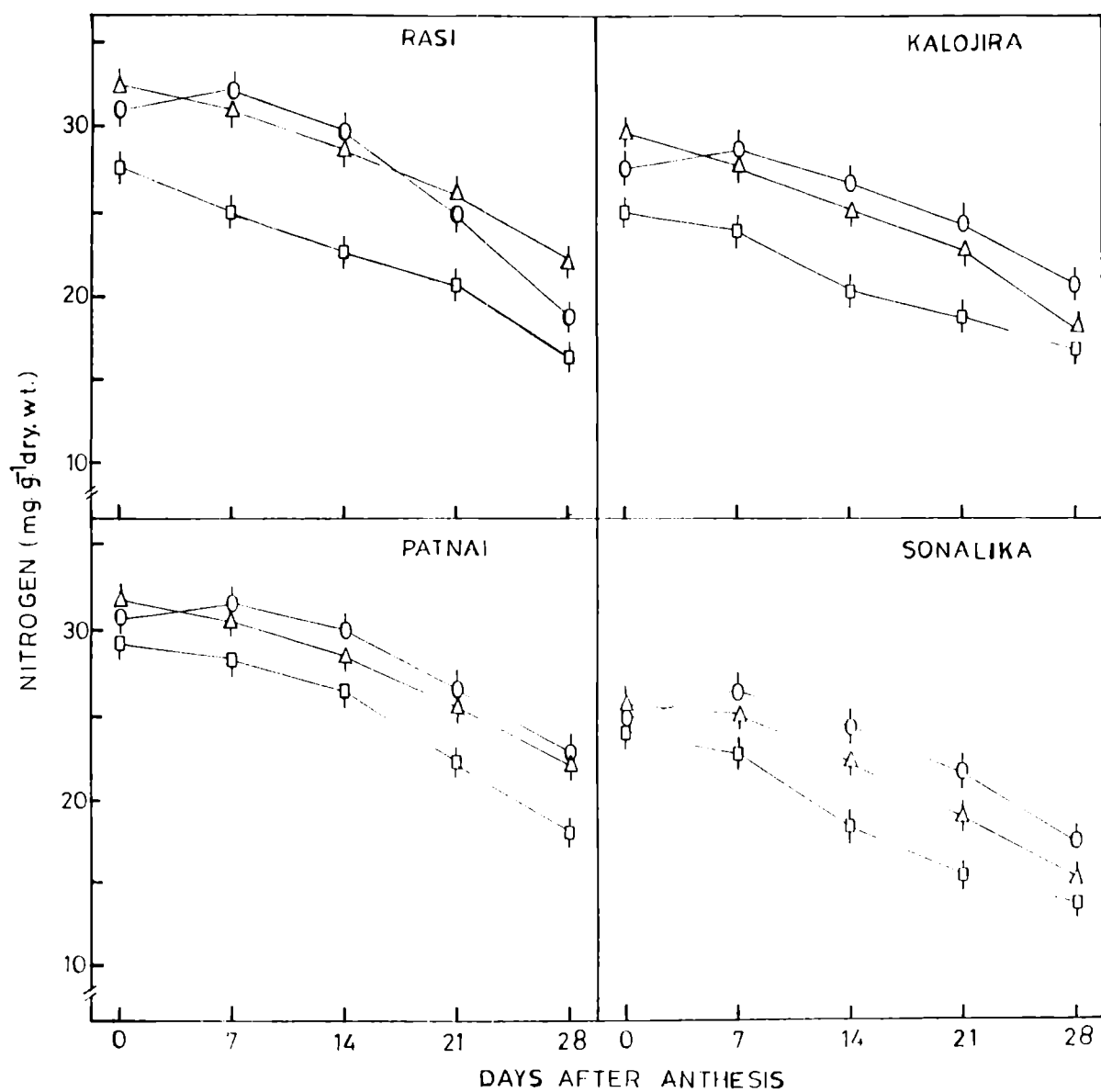


Fig.8. Changes in nitrogen content in the flag (○—○), second (△—△) and third (□—□) leaf of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

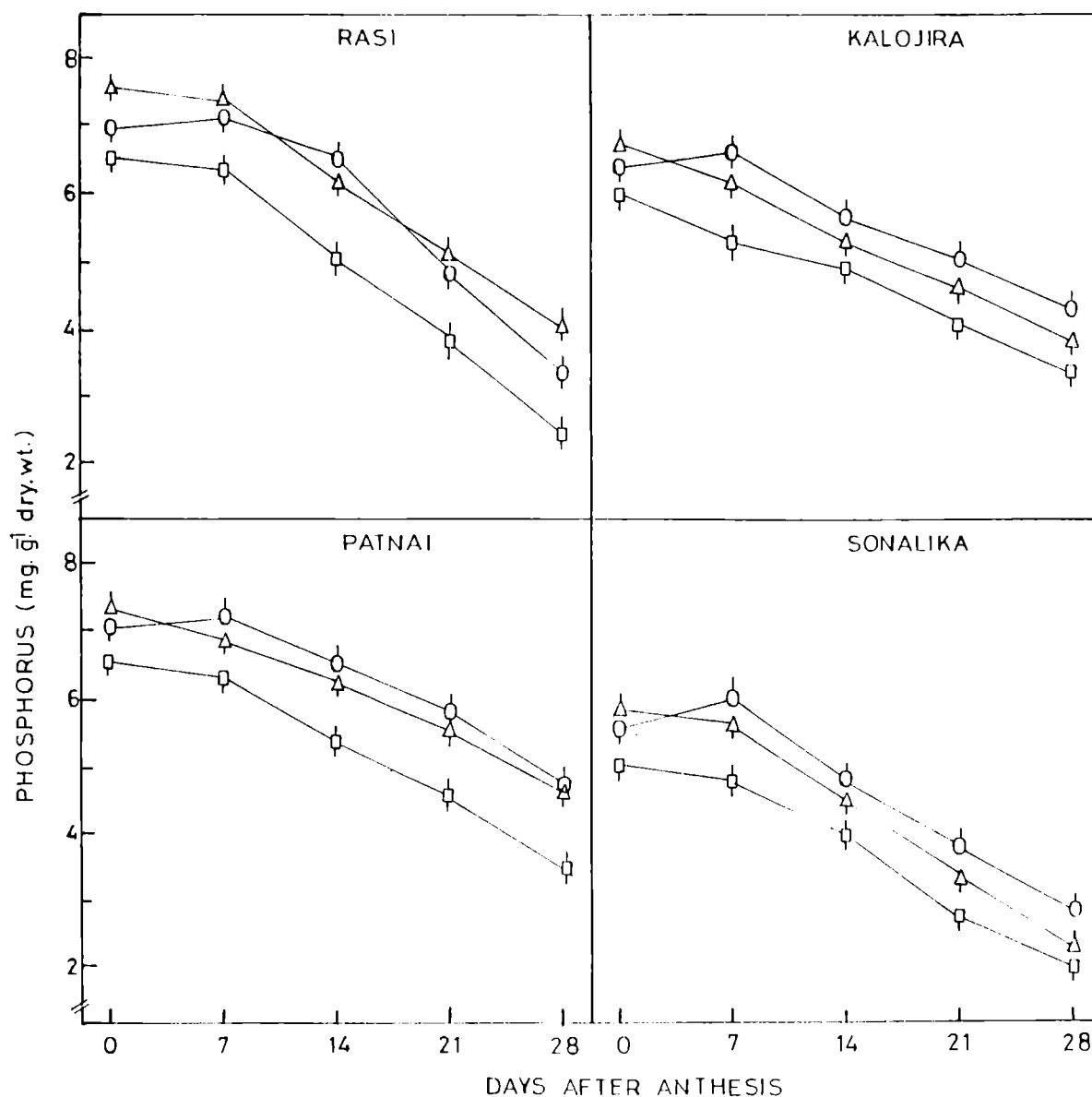


Fig.9. Changes in phosphorus content in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

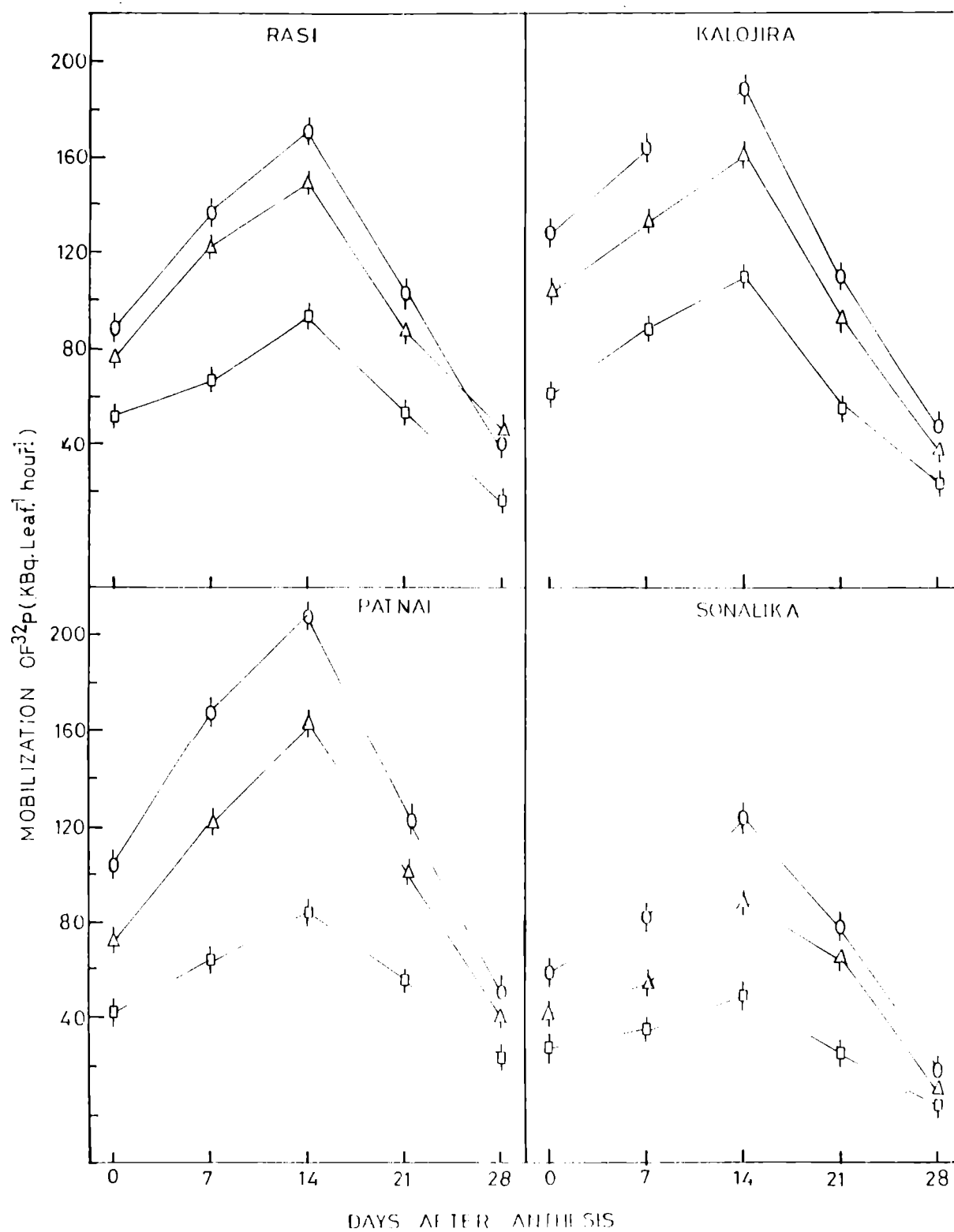


Fig.10. Changes in mobilization of $[^{32}\text{P}]$ -phosphate from the whole flag (○—○), second (△—△) and third (□—□) leaf to the grains of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

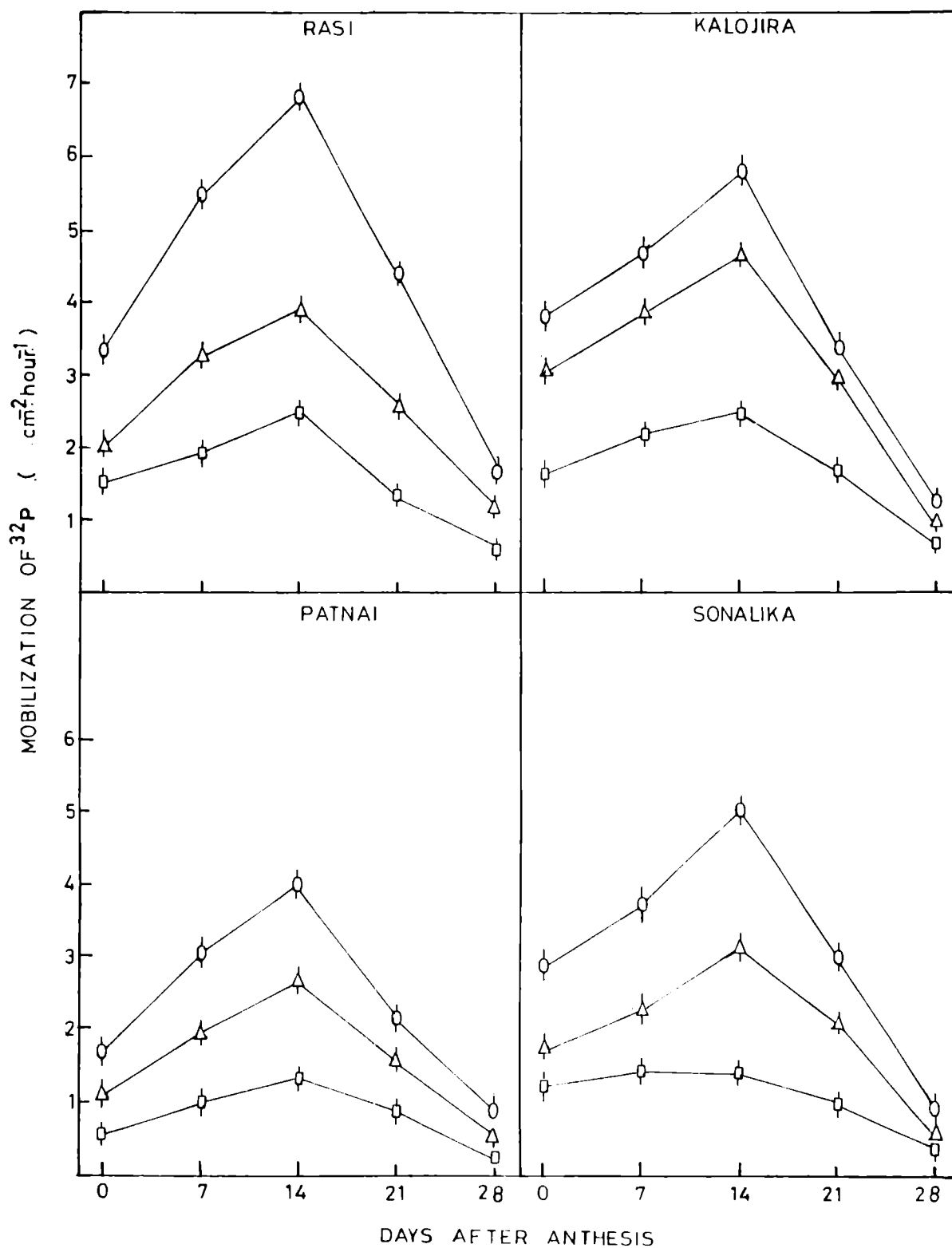


Fig.11. Changes in mobilization of [^{32}P]-phosphate on unit leaf area basis from the flag (○—○), second (△—△) and third (□—□) leaf to the grains of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

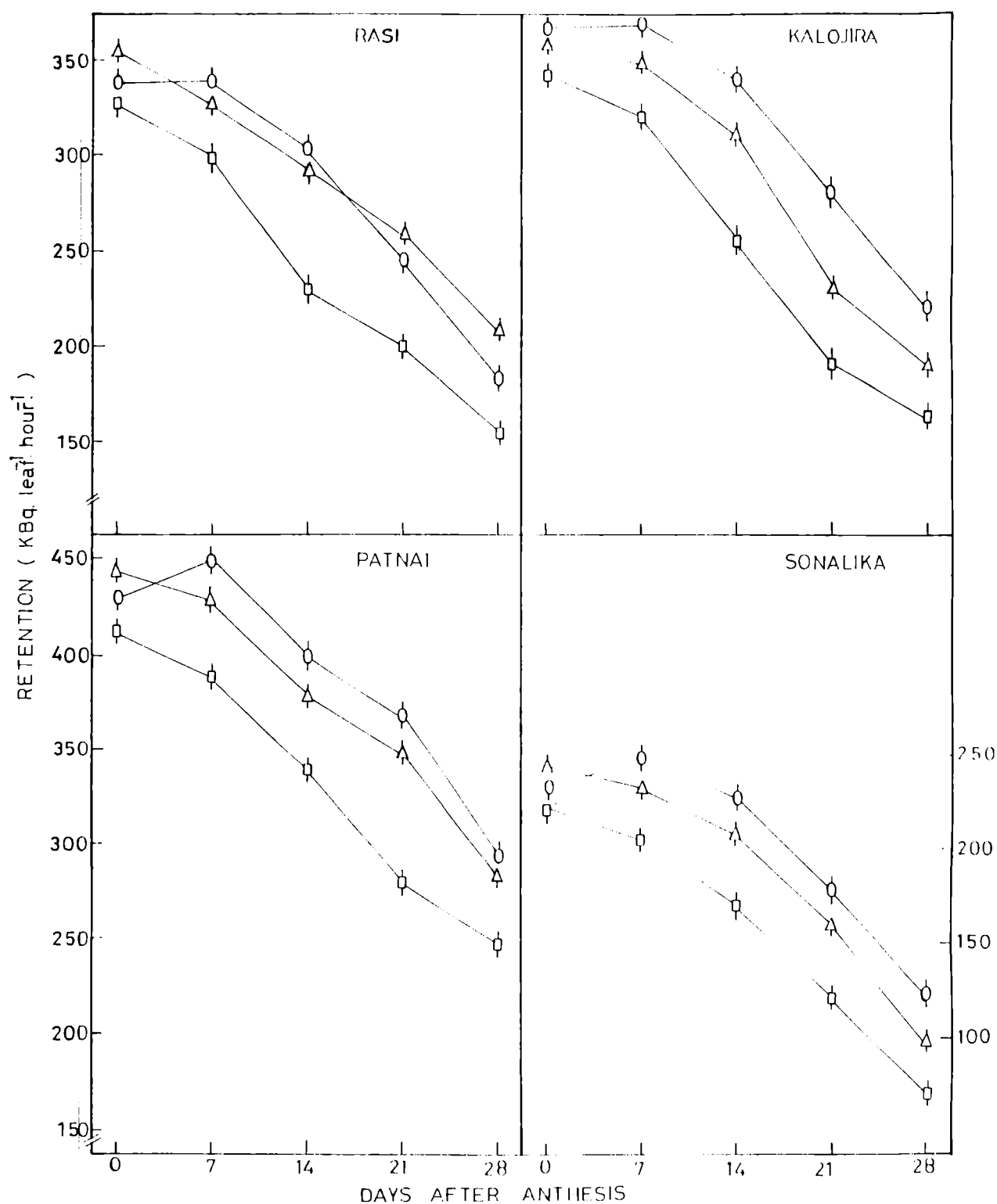


Fig.12. Changes in retention of $[^{32}\text{P}]$ -phosphate in the flag (○—○), second (△—△) and third (□—□) leaf of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

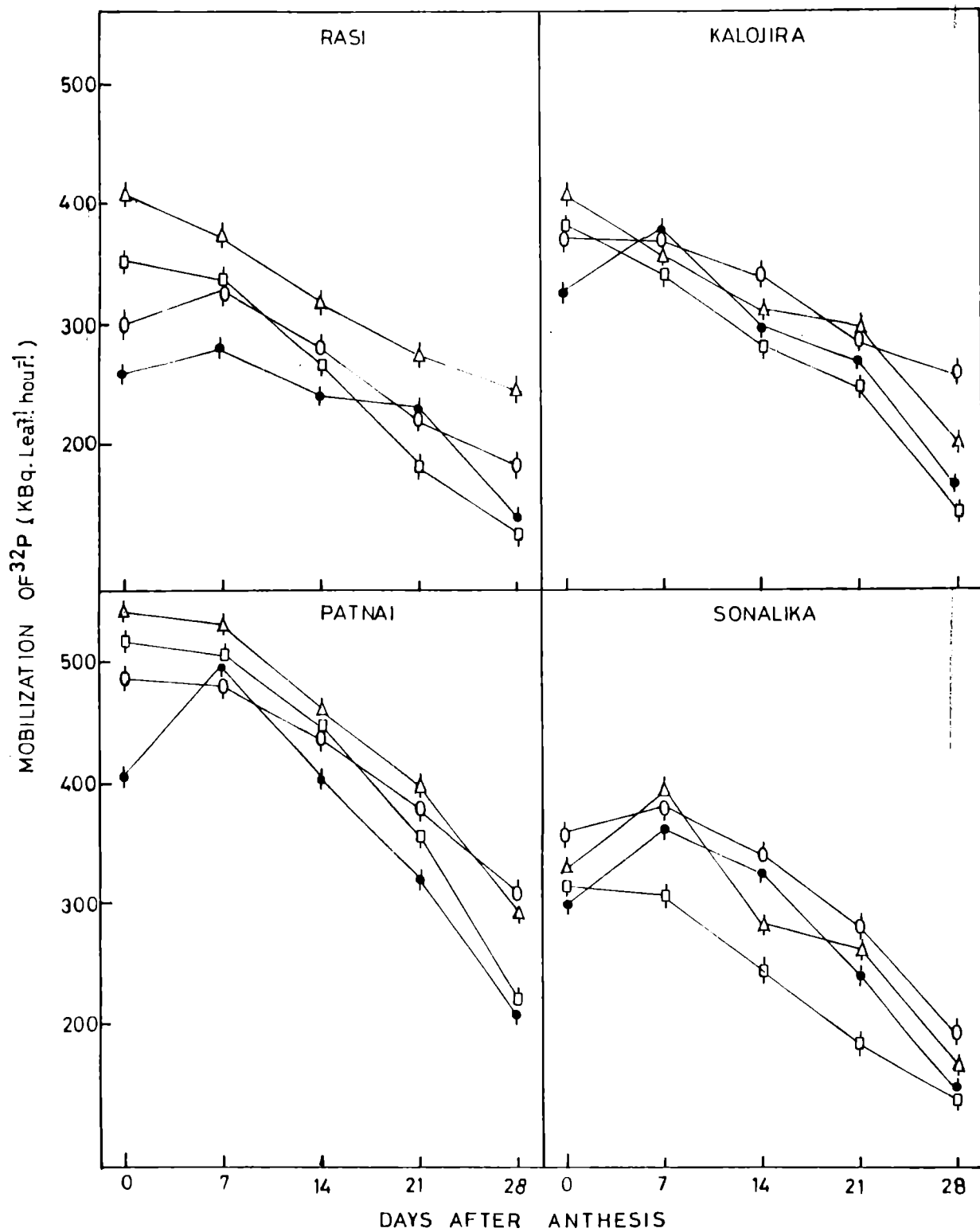


Fig.13. Changes in the export of [^{32}p]-phosphate from the roots to the flag (○—○), second (△—△) and third (□—□) leaf and grains (●—●) of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

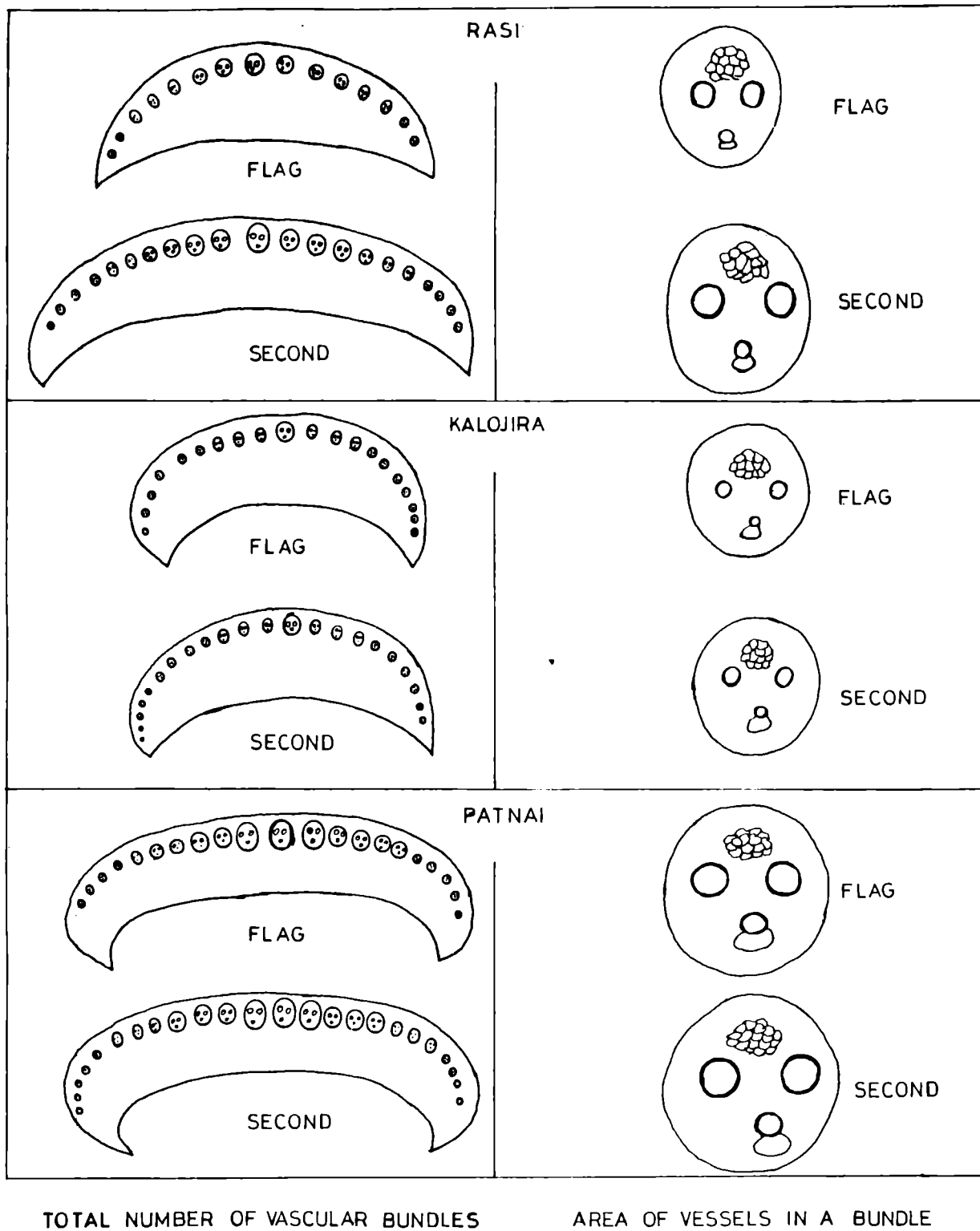


Fig.14. Diagrammatic representation of total number of vascular bundles and area of the xylem vessels in a bundle at the juncture of leaf lamina and leaf sheath of the flag and second leaf of three rice cultivars.

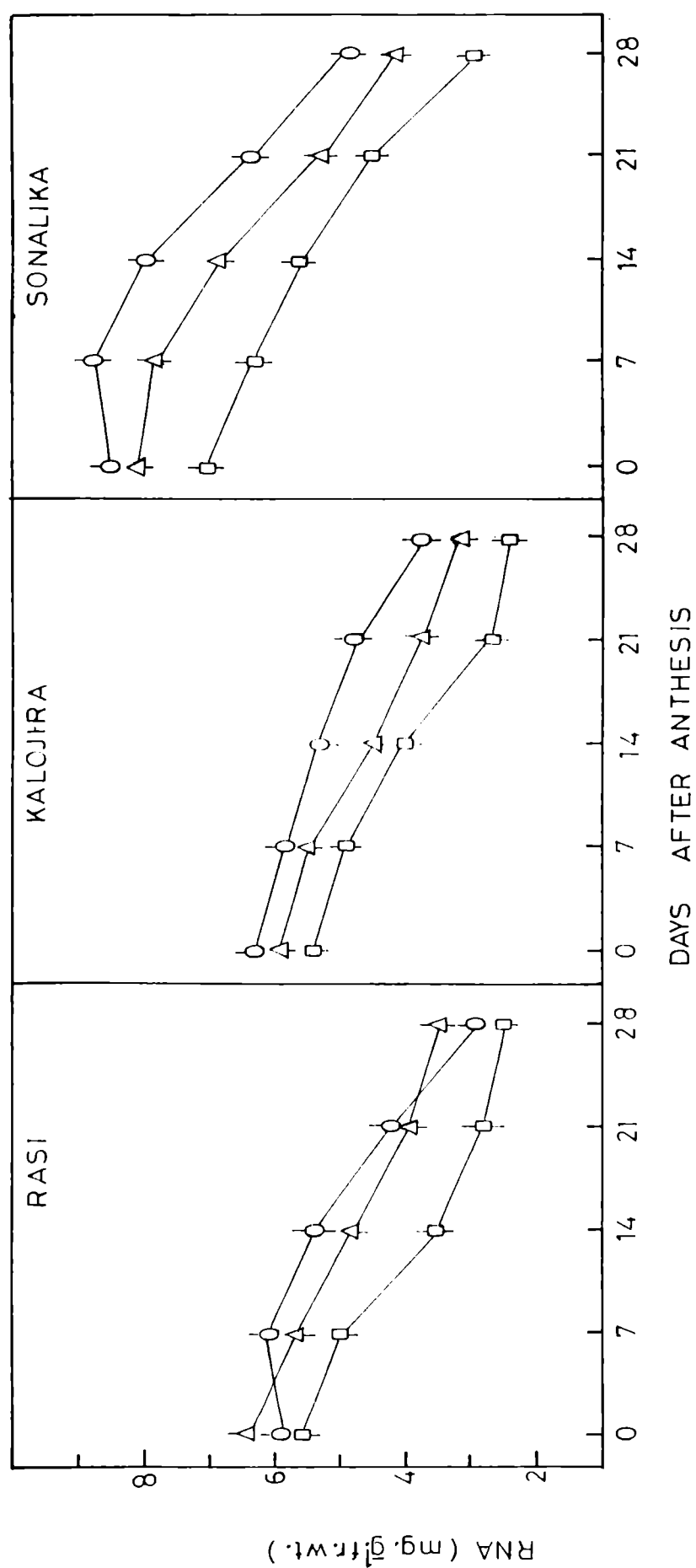


Fig.15. Changes in the contents of RNA in the flag (○—○), second (△—△) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

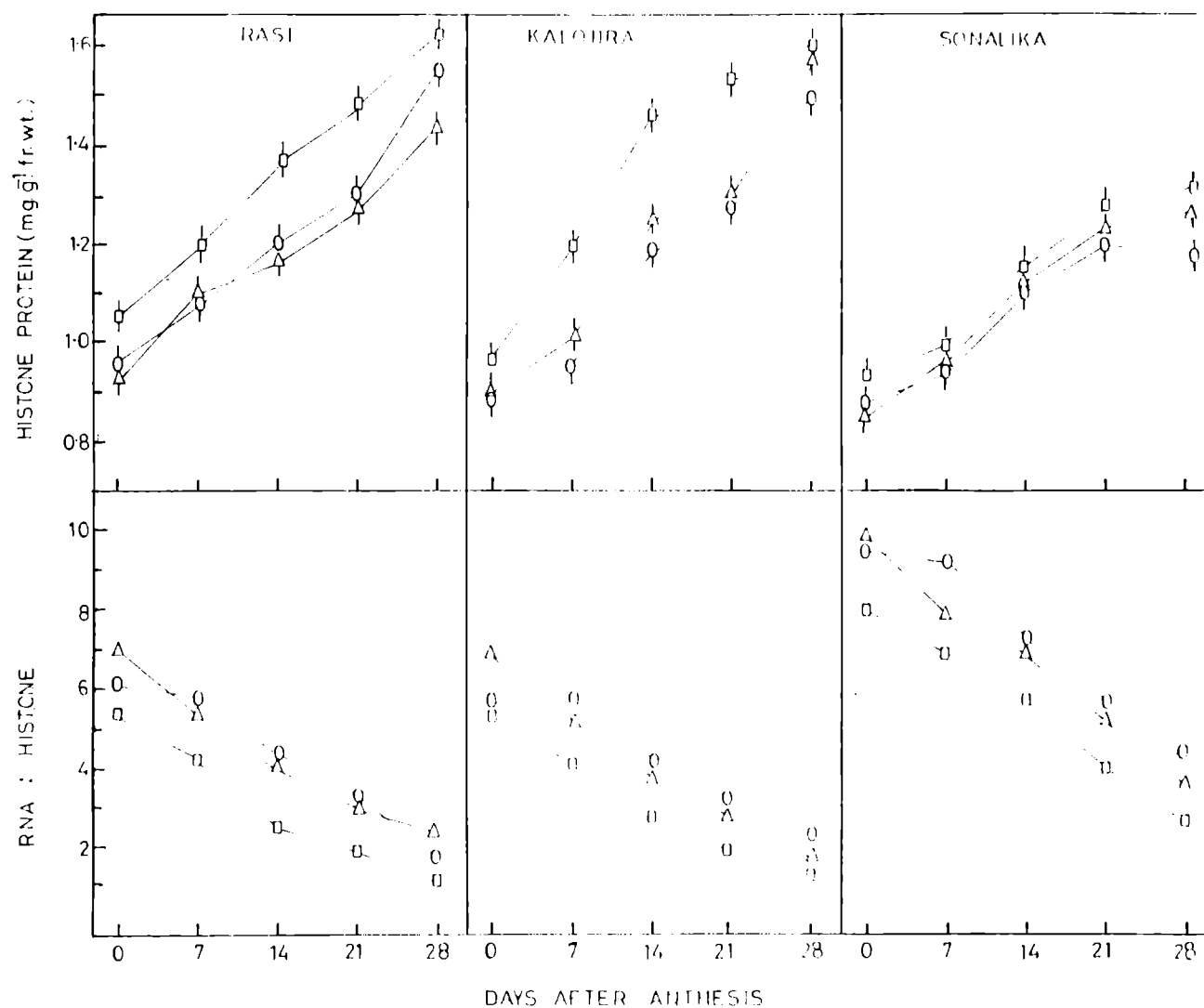


Fig.16. Changes in the content of histone protein and the ratio of RNA and histone in the flag (○—○), second (△—△) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

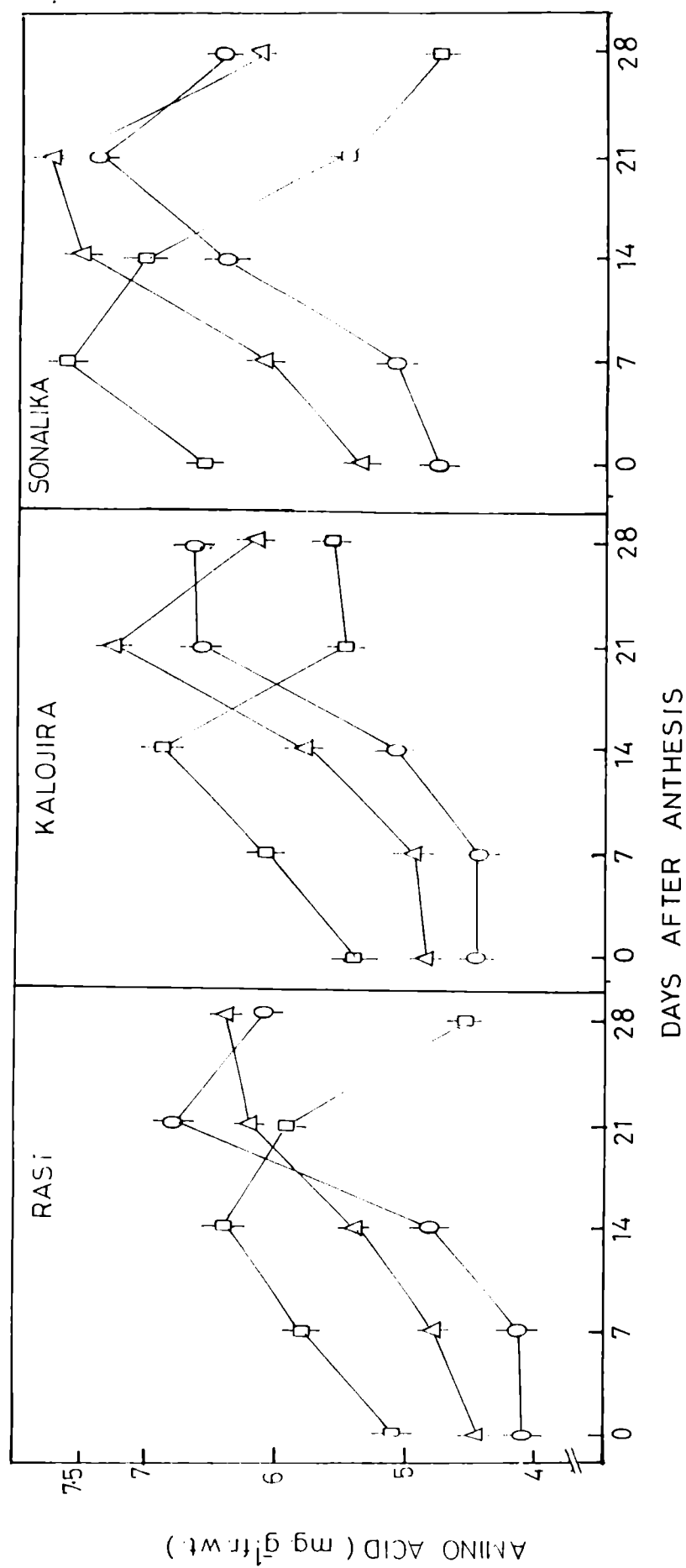


Fig.17. Changes in the accumulation of free amino acids in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

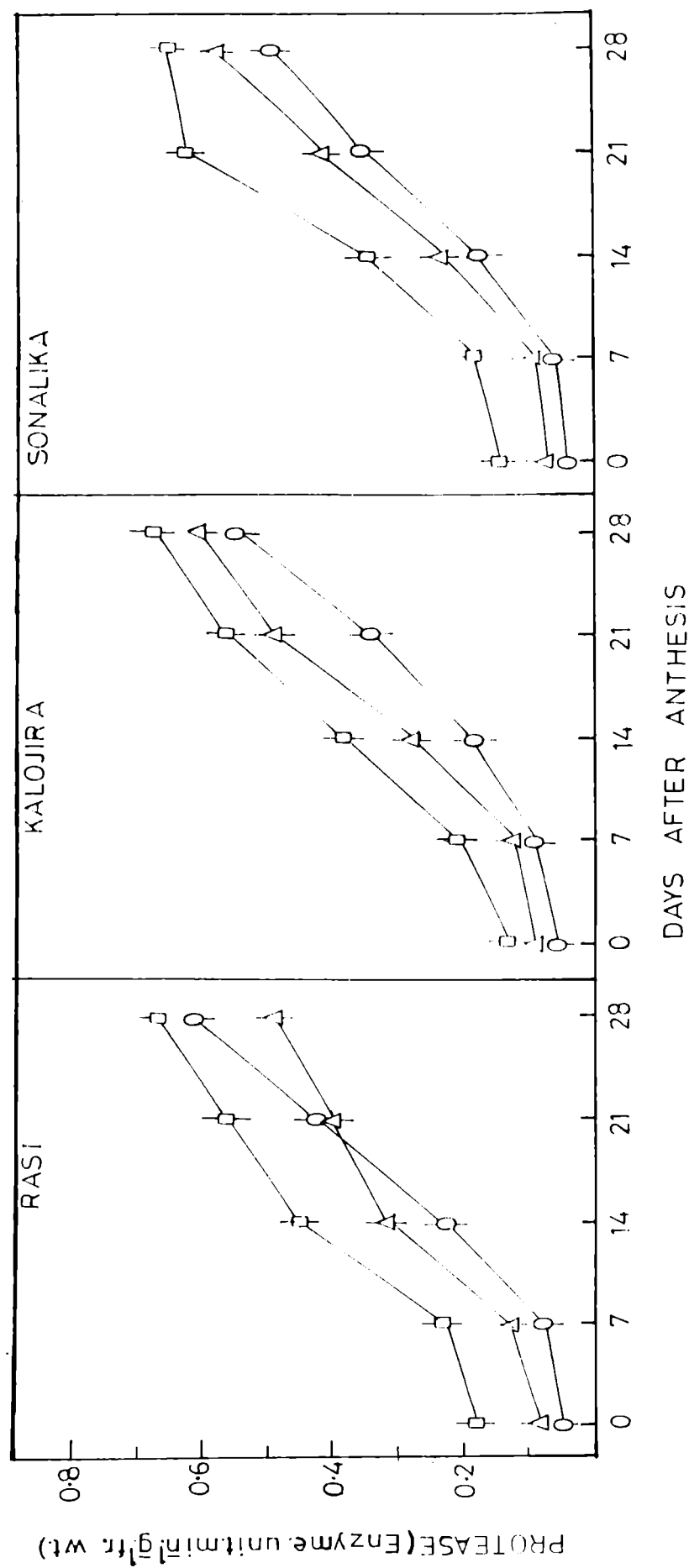


Fig.18. Changes in the protease activity in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

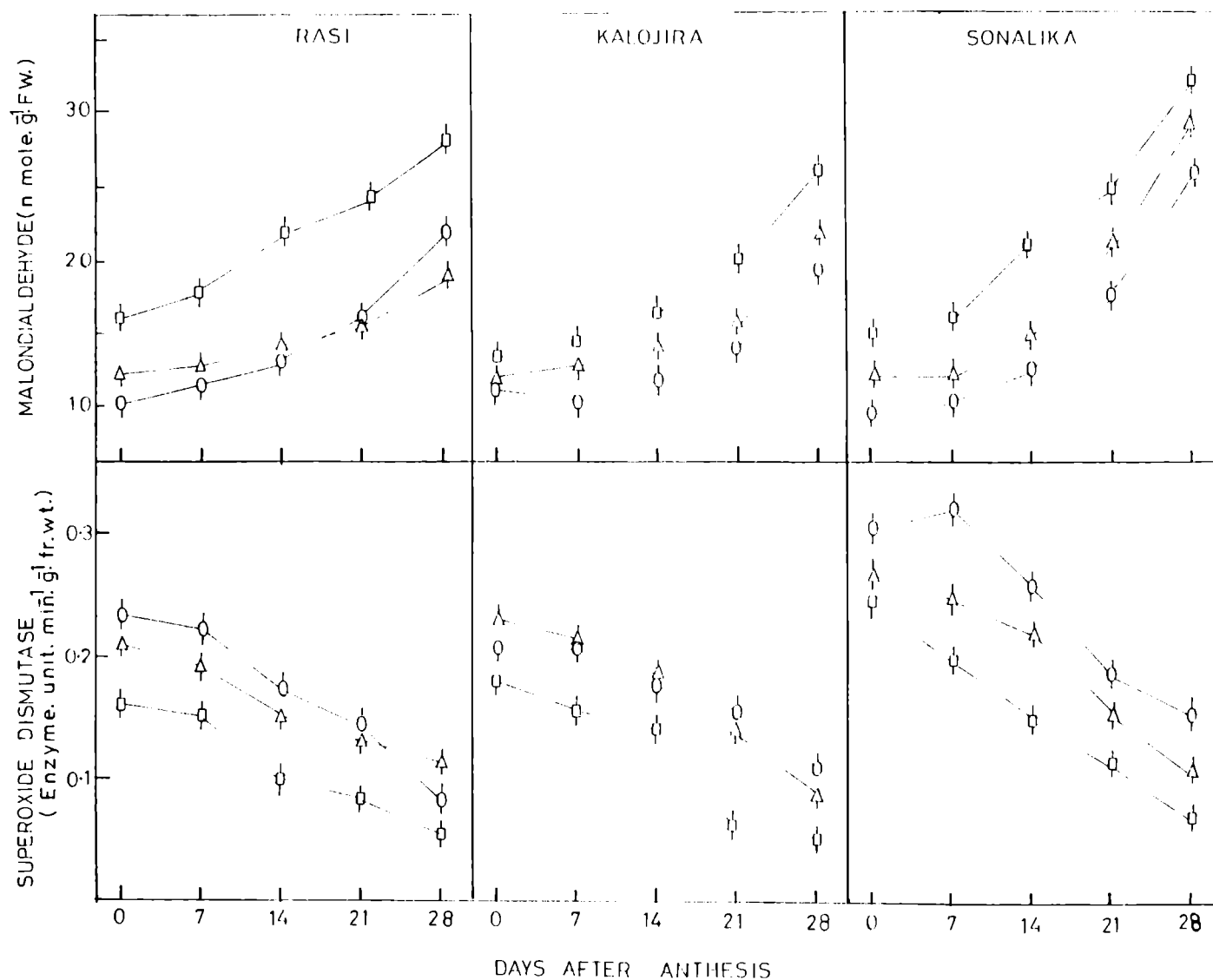


Fig.19. Changes in the content of malondialdehyde and the activity of superoxide dismutase in the flag (○—○), second (△—△) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

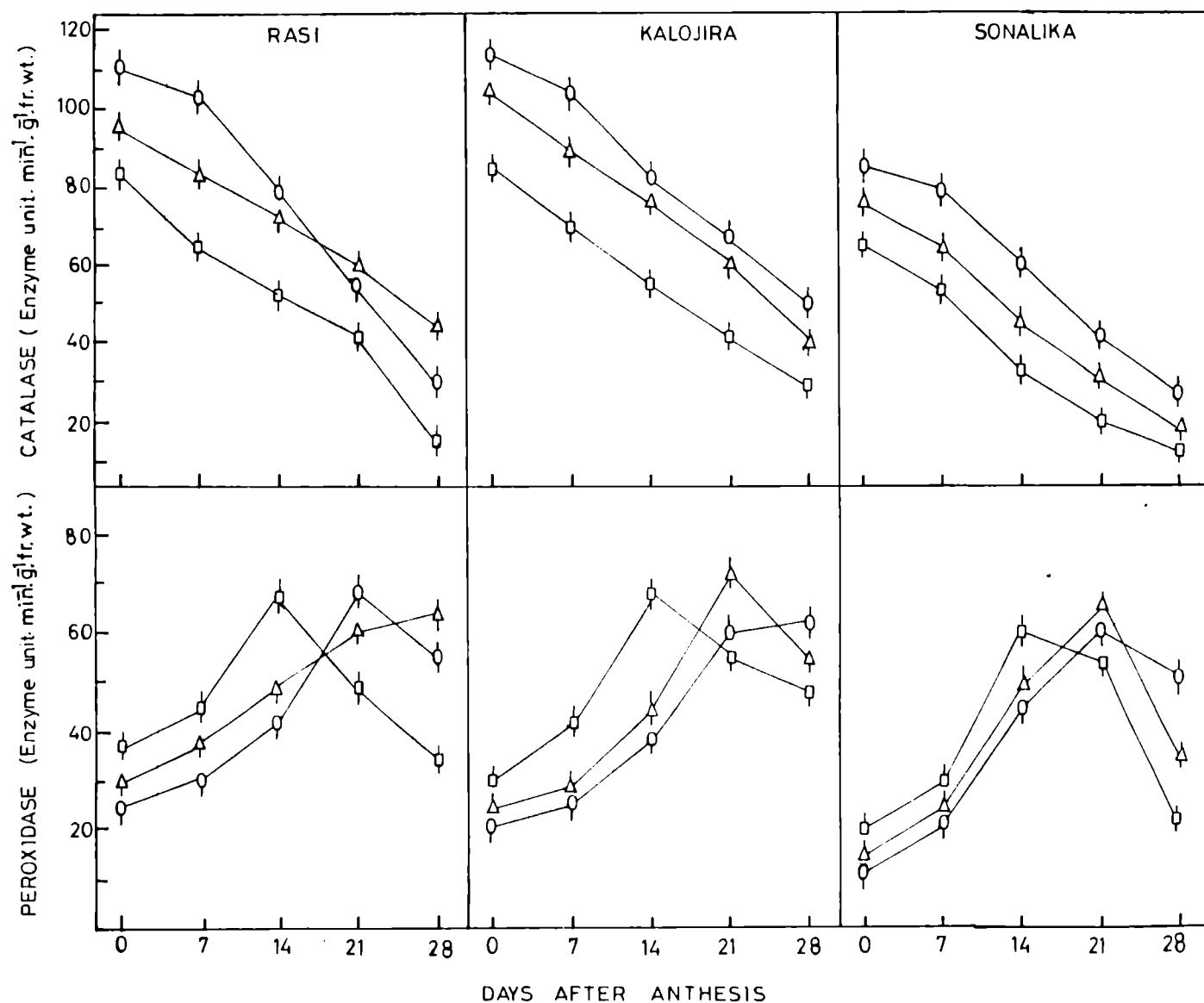


Fig.20. Changes in the activity of catalase and peroxidase in the flag (○—○), second (△—△) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

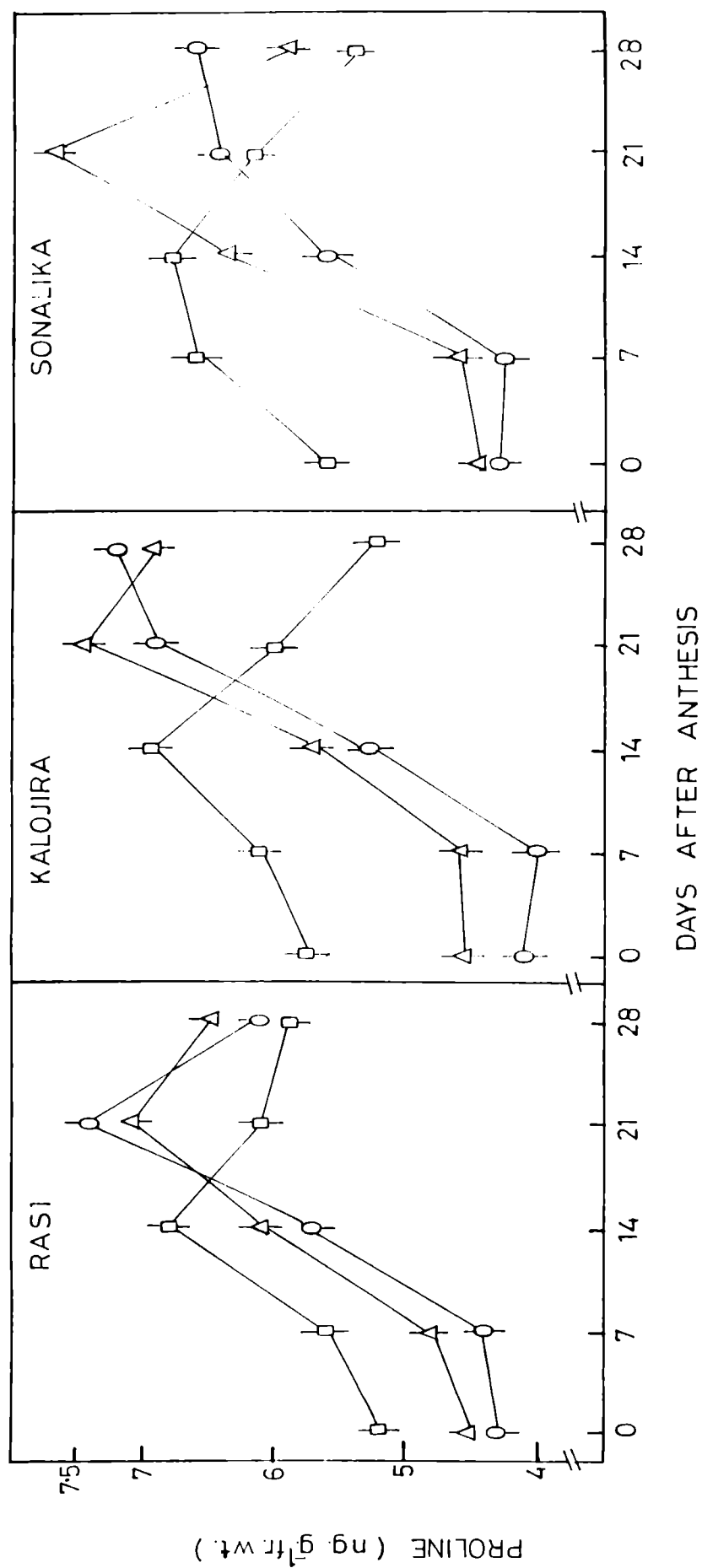


Fig.21. Changes in the accumulation of proline in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

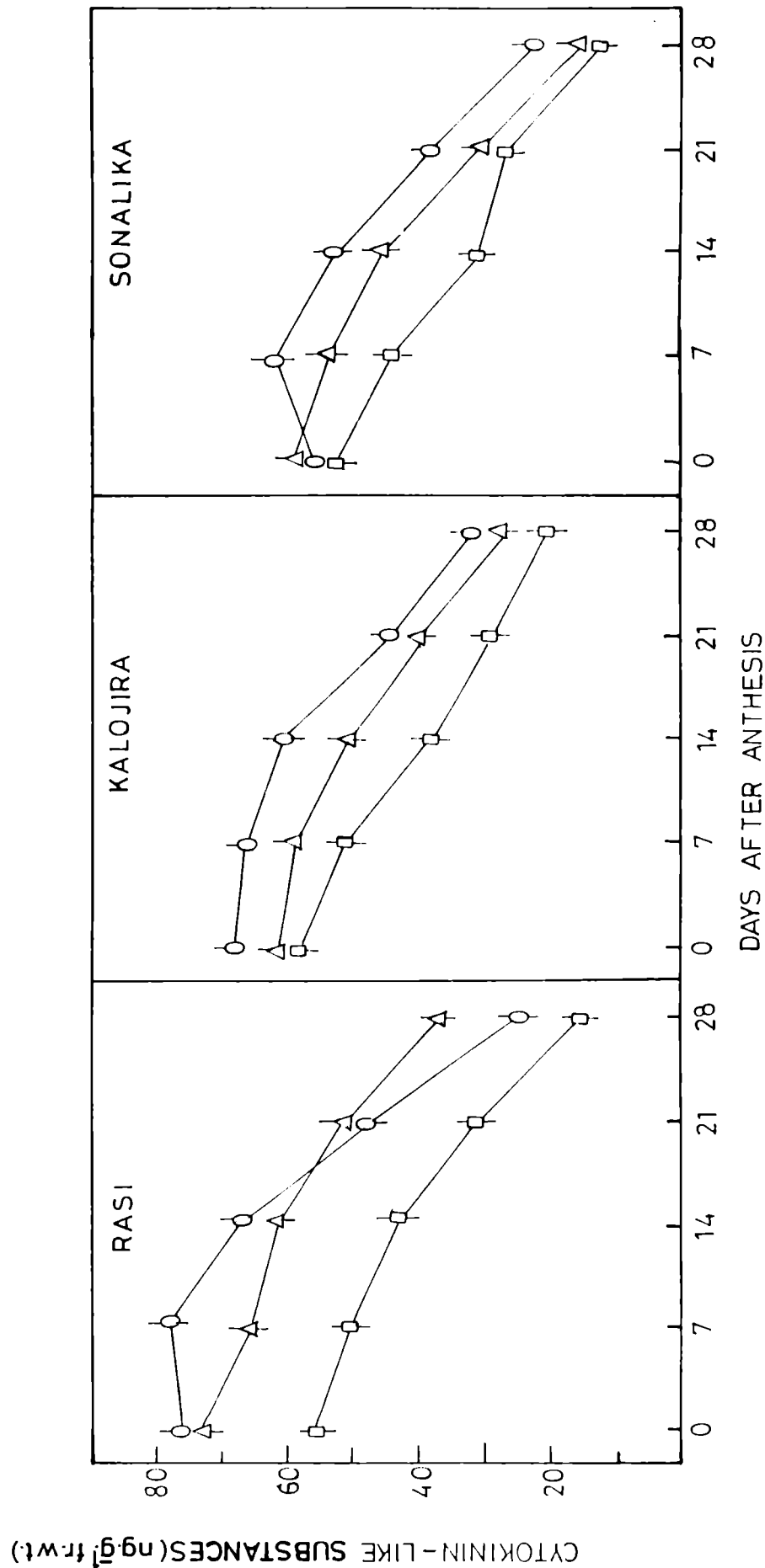


Fig.22. Changes in the content of endogenous cytokinin-like substances in the flag (), second () and third () leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

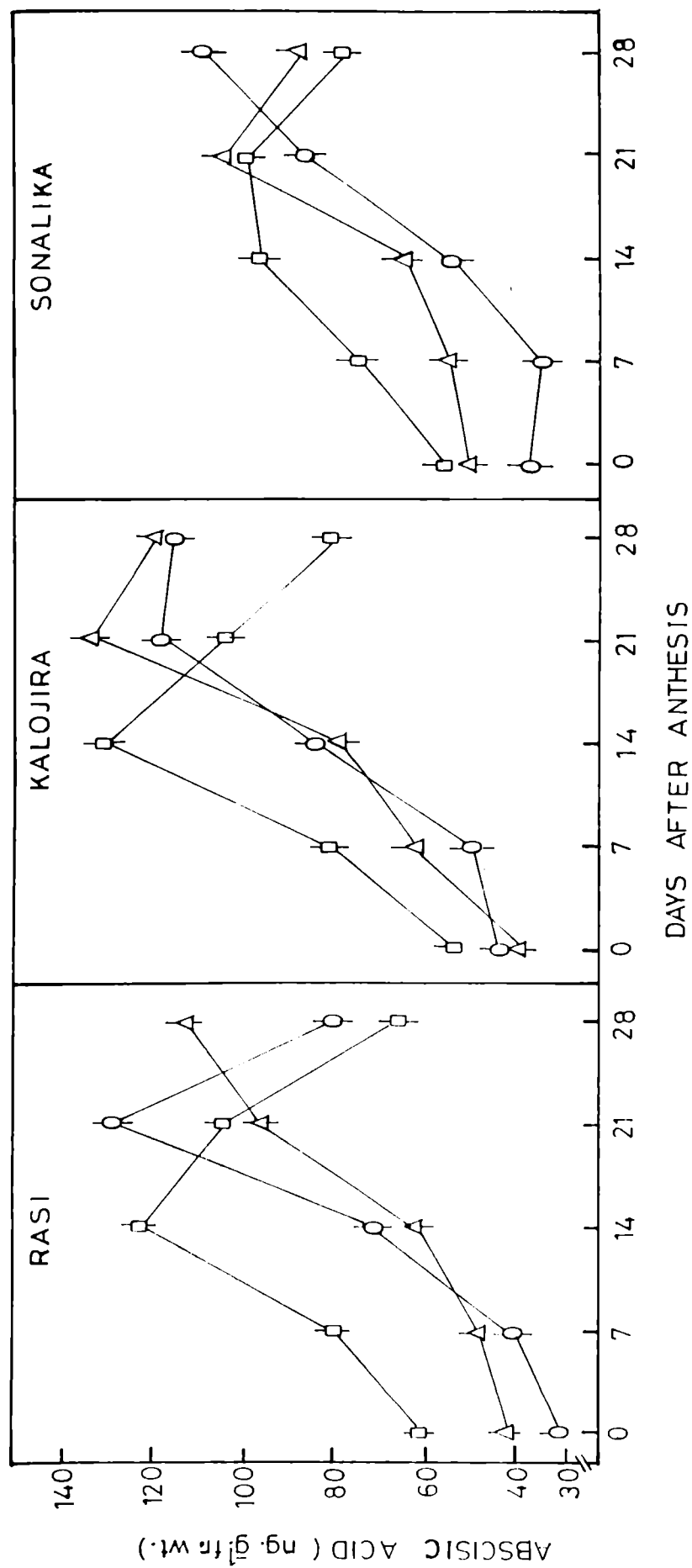


Fig.23. Changes in the content of endogenous abscisic acid in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

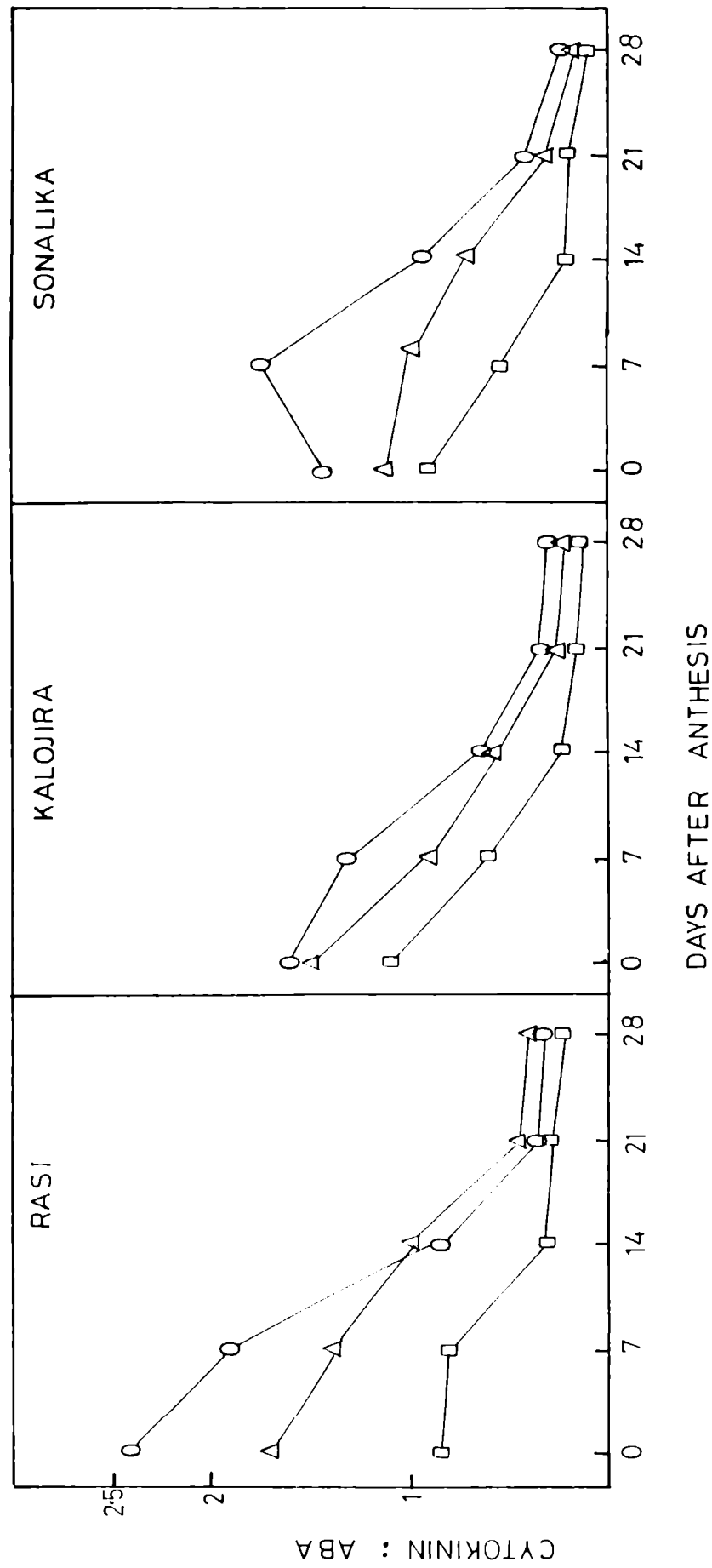


Fig.24. Changes in the ratio of cytokinin-like substances to abscisic acid in the flag (O—O), second (Δ—Δ) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development.

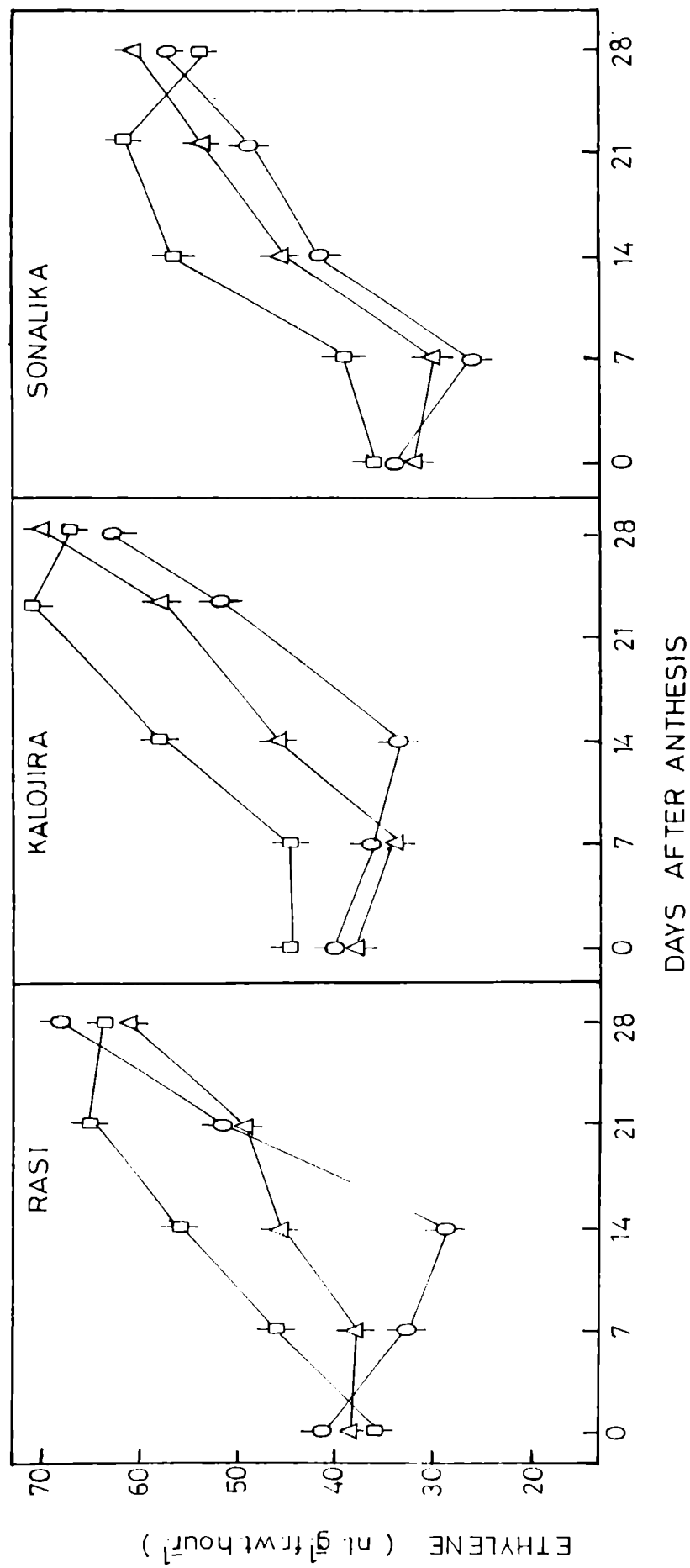


Fig.25. Changes in the evolution of endogenous ethylene from the flag (○—○), second (Δ—Δ) and third (□—□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

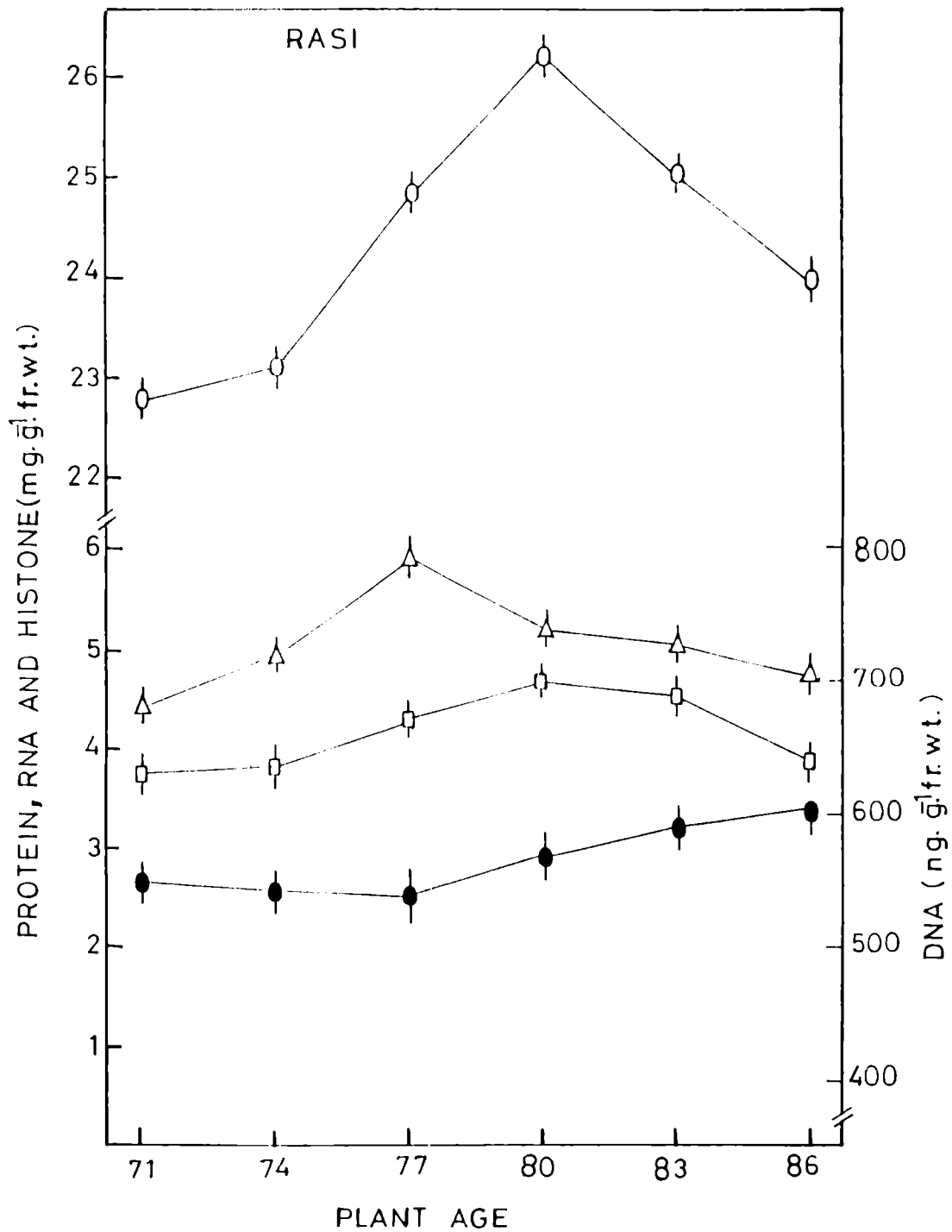


Fig.26. Changes in the content of total protein (○—○), RNA (△—△), DNA (□—□) and histone protein (●—●) in the shoot apex of Rasi rice cultivar prior to panicle emergence. Bars as in Fig.1.

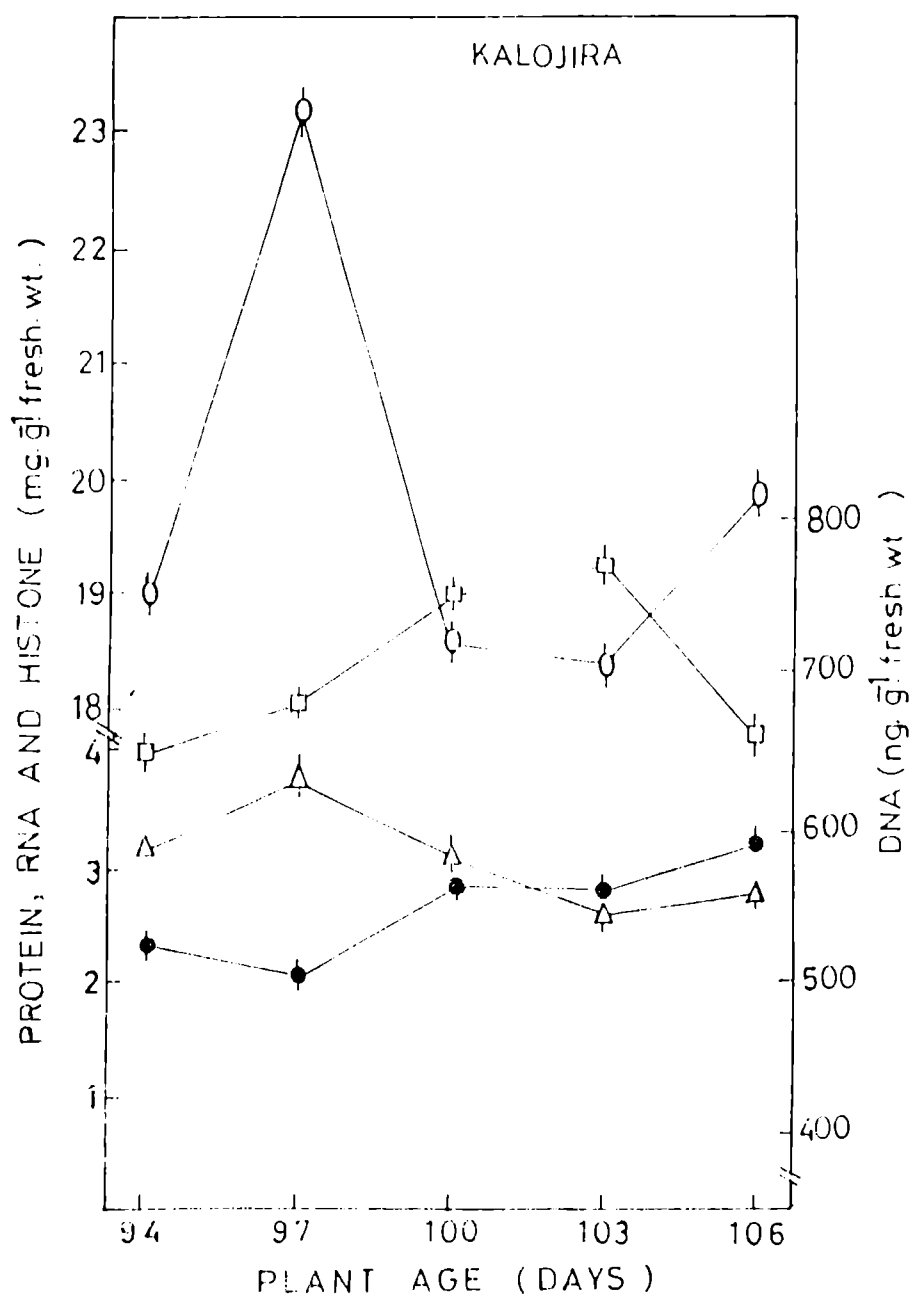


Fig.27. Changes in the content of total protein (O—O) , RNA (Δ — Δ) , DNA (\square — \square) and histone protein (\bullet — \bullet) in the shoot apex of Kalojira rice cultivar prior to panicle emergence. Bars as in Fig.1.

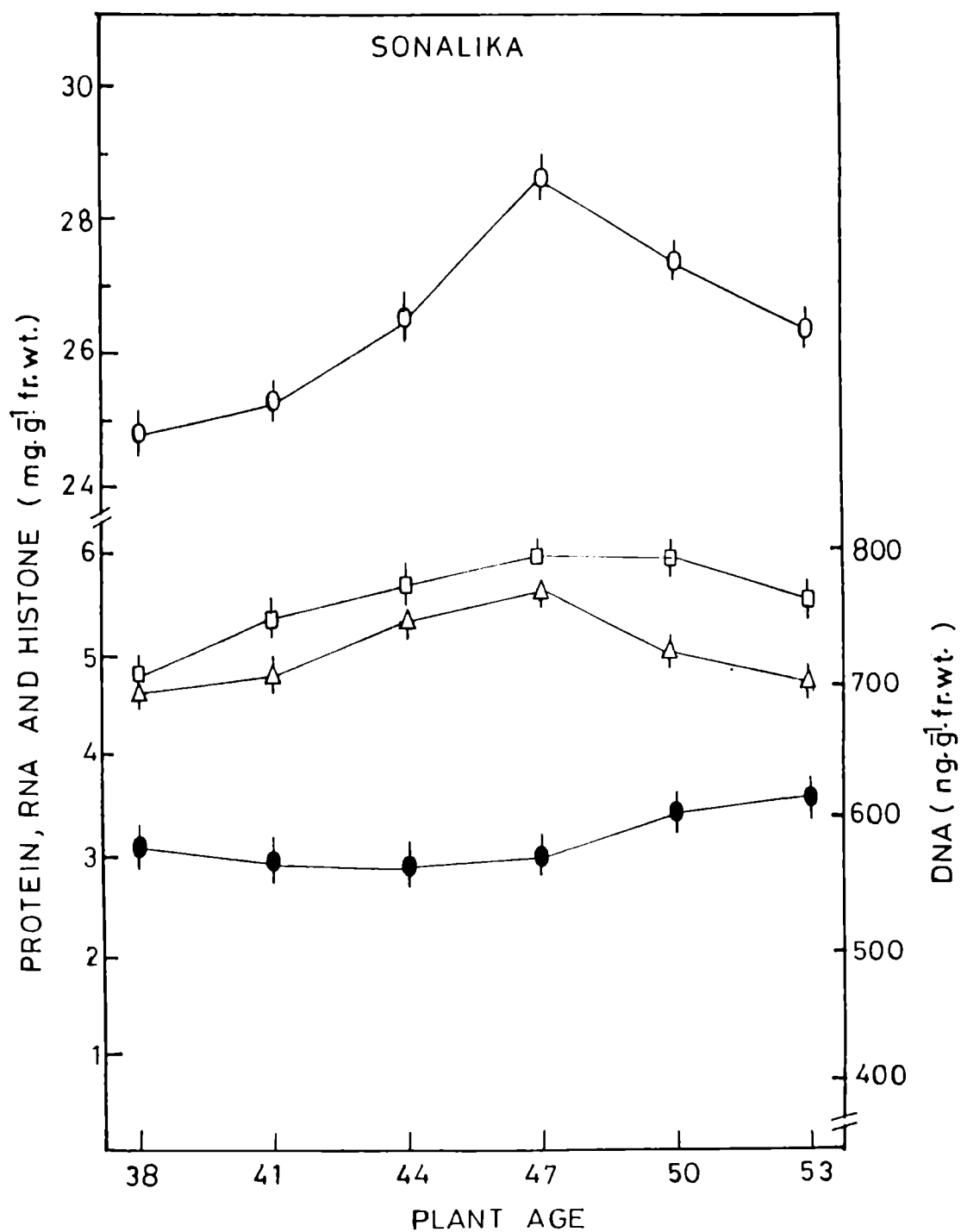


Fig.28. Changes in the content of total protein (○—○), RNA (△—△), DNA (□—□) and histone protein (●—●) in the shoot apex of Sonalika wheat cultivar prior to panicle emergence. Bars as in Fig.1.

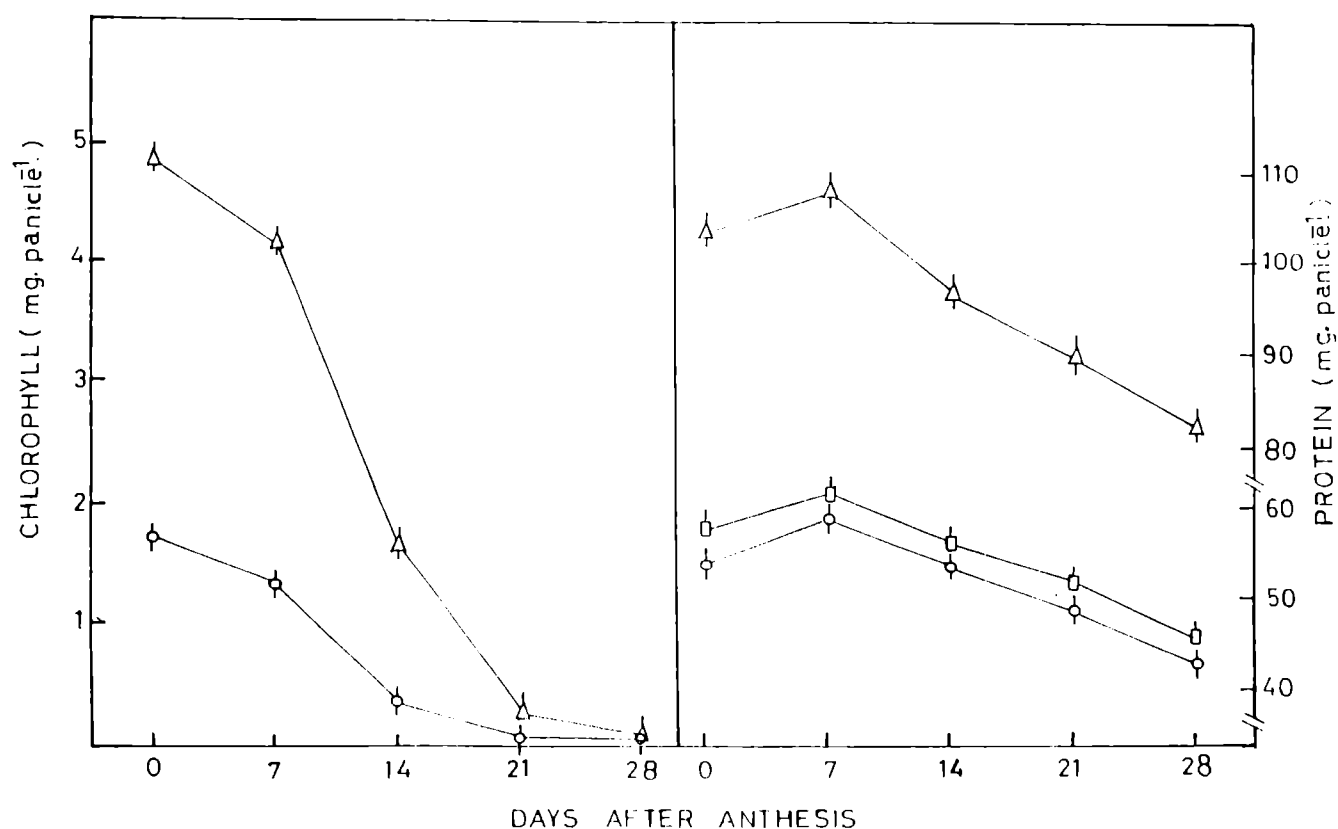


Fig.29. Changes in the content of chlorophyll and protein in the glumes of rice [Rasi (○—○), Kalojira (□—□)] and wheat [Sonalika (△—△)] cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

(N.B: The data of chlorophyll of Kalojira rice cultivar are not given here due to its very small amount.)

★ **TABLES** ★

Table 1. Total panicle weight and leaf area of different rice and wheat cultivars

Species	Cultivar	Total panicle weight (g)	Total leaf area (cm ²)		
			Flag	Second	Third
Rice	Rasi	1.920	26	40	36
	Sashyasri	1.840	28	42	37
	Kalojira	2.450	32	33	29
	Badsabhog	2.150	34	36	32
	Patnai	3.500	64	70	63
	Kalma	4.200	60	67	61
Wheat	Sonalika	2.150	20	25	23
	Kalyansona	2.000	18	22	24
LSD at P = 0.05		0.449	1.49	2.30	2.94

Table 2. Plant height, mode of senescence, number of vascular bundles, area of xylem vessels of a bundle and area of the lumen of the largest xylem vessel in rice and wheat cultivars

Species	Cultivar	Plant height (cm)	Mode of senescence	Number of vascular bundles/t.s.		Area of xylem vessels in a bundle (μm^2)		Area of the largest vessel (μm^2)	
				Flag leaf	Second leaf	Flag leaf	Second leaf	Flag leaf	Second leaf
Rice	Rasi	(79-82)	Non-sequential	15	21	118.3	133.6	50.1	63.4
	Kalojira	(101-103)	Sequential	20	22	75.0	81.0	42.9	45.6
	Patnai	(118-121)	Intermediate	21	25	171.0	182.0	84.9	99.6
Wheat	Sonalika	(75-80)	Sequential	21	20	56.0	63.0	28.0	31.0
LSD at P = 0.05				2.8	2.2	3.8	5.3	2.9	4.2

Table 3. Effect of benzyladenine on chlorophyll (Chl) and protein (Prot) contents (mg.g⁻¹ F.W) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

Species	Cultivar	Treatment	Leaf position	Days after anthesis									
				7			14			21			28
				Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.		
Rice	Rasi	Control	Flag	1.21	83.4	0.77	68.6	0.56	60.6	0.20	43.4		
			Second	1.18	78.1	0.72	65.5	0.54	58.3	0.29	48.0		
			Third	0.82	64.2	0.60	56.3	0.25	49.5	0.05	41.0		
		BA	Flag	1.22	82.2	0.89	71.0	0.64	65.0	0.34	50.0		
			Second	1.20	78.9	0.84	69.0	0.58	60.0	0.38	53.3		
			Third	0.82	64.5	0.72	58.8	0.33	53.2	0.09	45.7		
	Kalojira	Control	Flag	0.006	2.64	0.006	1.69	0.008	2.82	0.0084	2.80		
			Second	1.16	82.0	0.76	69.6	0.52	59.0	0.31	46.0		
			Third	0.89	74.0	0.70	63.0	0.48	54.0	0.21	43.3		
		BA	Flag	0.73	64.0	0.54	56.0	0.23	49.0	0.08	39.5		
			Second	1.09	82.8	0.81	70.9	0.56	63.0	0.37	53.0		
			Third	0.91	74.5	0.75	66.0	0.53	58.5	0.31	48.5		
Wheat	Sonalika	Control	Flag	0.74	66.5	0.57	60.0	0.29	54.0	0.12	44.0		
			Second	0.004	1.96	0.001	2.0	0.03	2.68	0.06	1.84		
			Third	1.10	65.5	0.70	59.0	0.58	48.5	0.21	38.0		
		BA	Flag	0.92	62.2	0.69	54.5	0.49	45.0	0.12	34.0		
			Second	0.79	57.2	0.53	48.0	0.32	38.8	0.04	31.0		
			Third	1.14	71.0	0.84	62.5	0.64	56.0	0.31	44.4		
	LSD at P = 0.05	Control	Flag	0.99	66.0	0.71	58.0	0.55	53.5	0.26	42.0		
			Second	0.75	58.5	0.56	54.0	0.36	46.0	0.06	37.5		
			Third	0.0085	1.33	0.09	1.08	0.01	2.9	0.009	1.88		

Table 4. Effect of gibberellic acid on chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} F.M.) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

Species	Cultivar	Treatment	Leaf position	Days after anthesis								
				7			14			21		
				Chl.	Prot.		Chl.	Prot.		Chl.	Prot.	
Rice	Rasi	Control	Flag	1.21	83.4		0.77	68.6		0.56	60.6	
			Second	1.18	78.1		0.72	65.5		0.54	58.3	
			Third	0.82	64.2		0.60	56.3		0.25	45.1	
		GA ₃	Flag	1.22	82.2		0.86	70.0		0.59	63.7	
			Second	1.16	79.6		0.80	66.6		0.55	60.8	
			Third	0.81	64.0		0.64	57.3		0.31	51.8	
	Kalojira	LSD at P = 0.05		0.002	0.58		0.02	0.84		0.008	2.84	
		Control	Flag	1.10	82.0		0.76	68.0		0.52	59.0	
			Second	0.89	74.5		0.70	63.0		0.48	58.0	
			Third	0.73	64.0		0.54	56.0		0.23	49.4	
		GA ₃	Flag	1.08	83.1		0.78	69.3		0.56	61.0	
			Second	0.91	75.8		0.72	64.2		0.52	59.0	
Wheat	Sonalika	Control	Third	0.76	65.6		0.55	57.7		0.32	51.5	
				0.012	0.46		0.009	1.2		0.006	1.62	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
		LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	
		GA ₃	Flag	1.10	65.5		0.70	59.0		0.58	48.5	
			Second	0.92	62.2		0.69	54.0		0.49	45.0	
			Third	0.79	57.2		0.52	48.0		0.32	38.8	
Wheat	Sonalika	Control	Flag	1.08	66.0		0.75	61.0		0.62	52.6	
			Second	0.93	63.0		0.69	55.3		0.51	50.0	
			Third	0.78	57.9		0.54	51.5		0.36	41.6	
	Sonalika	LSD at P = 0.05		0.004	0.48		0.04	0.64		0.012	1.06	

Table 5. Effect of abscisic acid on chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} F.W) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

Species	Cultivar	Treatment	Leaf position	Days after anthesis								
				7			14			21		
				Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.
Rice	Rasi	Control	Flag	1.21	83.4	0.77	68.6	0.56	60.6	0.20	43.4	0.20
			Second	1.18	78.1	0.72	65.5	0.54	58.3	0.29	48.0	0.29
			Third	0.82	64.2	0.60	56.3	0.25	49.1	0.05	41.0	0.05
		ABA	Flag	1.20	83.0	0.73	66.7	0.52	57.2	0.16	40.2	0.16
			Second	1.13	77.0	0.70	64.0	0.50	55.5	0.22	44.3	0.22
			Third	0.80	63.5	0.56	54.0	0.21	46.0	0.04	36.6	0.04
	Kalojira	LSD at P = 0.05		0.001	0.06	0.005	1.54	0.0046	0.34	0.002	1.32	0.002
	Control	Flag	Second	1.10	82.0	0.76	68.0	0.52	59.0	0.29	46.0	0.29
			Third	0.89	74.5	0.70	63.0	0.48	54.0	0.21	43.3	0.21
			Third	0.73	64.0	0.54	56.0	0.23	49.0	0.08	39.5	0.08
	ABA	Flag	Second	1.09	80.8	0.73	65.5	0.46	54.2	0.21	42.5	0.21
			Third	0.89	72.2	0.61	61.8	0.42	51.5	0.16	40.5	0.16
Wheat	Sonalika	Control	Flag	0.70	63.1	0.50	53.3	0.20	46.6	0.05	36.0	0.05
			Second	0.0025	0.62	0.004	1.25	0.0062	0.66	0.002	1.82	0.002
			Third	0.0025	0.62	0.004	1.25	0.0062	0.66	0.002	1.82	0.002
		ABA	Flag	1.10	65.5	0.70	59.0	0.58	48.5	0.21	38.0	0.21
			Second	0.92	62.2	0.69	54.0	0.49	45.0	0.12	34.0	0.12
			Third	0.79	57.2	0.52	48.0	0.32	38.8	0.04	31.0	0.04
	LSD at P = 0.05	Control	Flag	1.06	64.5	0.67	57.2	0.53	45.5	0.14	35.5	0.14
			Second	0.90	62.0	0.66	53.0	0.44	43.2	0.11	32.0	0.11
			Third	0.76	55.5	0.50	45.0	0.26	35.2	0.03	28.0	0.03
		ABA	Flag	0.0014	0.35	0.0065	0.69	0.022	1.49	0.002	0.68	0.002
			Second	0.0014	0.35	0.0065	0.69	0.022	1.49	0.002	0.68	0.002
			Third	0.0014	0.35	0.0065	0.69	0.022	1.49	0.002	0.68	0.002

Table 6. Effect of (BA + GA₃) on chlorophyll (Chl) and protein (Prot) contents (mg.g⁻¹ F.W) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

Species	Cultivar	Treatment	Lear position	Days after anthesis							
				7		14		21		28	
				Chl.	Prot.	Chl.	Prot.	Chl.	Prot.		
Rice	Rasi	Control	Flag	1.21	83.4	0.77	68.6	0.56	60.6	0.20	43.4
			Second	1.18	78.1	0.72	65.5	0.54	58.3	0.29	48.0
			Third	0.82	64.2	0.60	56.3	0.25	49.1	0.05	41.0
		BA + GA ₃	Flag	1.25	84.2	0.91	74.2	0.66	65.5	0.37	51.8
			Second	1.19	79.5	0.82	69.0	0.61	64.0	0.40	54.1
			Third	0.82	65.5	0.61	59.6	0.33	55.4	0.07	44.4
	LSD at P = 0.05			0.012	00.49	0.003	2.10	0.009	2.10	0.0074	1.62
	Kalojira	Control	Flag	1.10	82.0	0.76	68.0	0.52	59.0	0.29	46.0
			Second	0.89	74.5	0.70	63.0	0.48	54.0	0.21	43.3
			Third	0.73	64.0	0.54	56.0	0.23	49.0	0.08	39.5
		BA + GA ₃	Flag	1.10	83.0	0.84	72.2	0.58	64.5	0.39	54.8
			Second	0.87	75.5	0.76	67.0	0.53	59.0	0.33	50.3
Third			0.73	65.9	0.56	61.5	0.30	56.0	0.11	44.5	
LSD at P = 0.05			0.001	0.54	0.0063	0.95	0.0069	1.94	0.009	0.56	
Wheat	Sonalika	Control	Flag	1.10	65.5	0.70	59.0	0.58	48.5	0.21	38.0
			Second	0.92	62.2	0.69	54.0	0.49	45.0	0.12	34.0
			Third	0.79	57.2	0.52	48.0	0.32	38.8	0.04	31.0
		BA + GA ₃	Flag	1.12	69.5	0.81	63.4	0.63	59.0	0.32	48.5
			Second	0.94	64.2	0.74	59.5	0.56	56.3	0.29	45.5
			Third	0.80	57.0	0.58	55.0	0.36	47.3	0.07	38.0
	LSD at P = 0.05			0.004	0.49	0.0067	1.72	0.013	1.16	0.0073	2.80

Table 7. Effect of benzyladenine on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 8 & 9.

Species	Cultivar	Leaf position	Days after anthesis												
			7			14			21			28			
			N	P		N	P		N	P		N	P		
Rice		Flag	+1.25	+2.7		+1.8	+6.4		+8.2	+16.0		+15.2	+37.0		
	Rasi	Second	+0.96	+1.8		+1.6	+6.6		+15.2	+12.0		+10.0	+23.9		
		Third	+2.0	+2.0		+5.6	+8.3		+ 9.1	+20.0		+15.5	+34.0		
		Kalojira	Flag	+0.70	+0.83		+3.6	+5.1		+ 4.6	+ 7.6		+ 9.2	+16.0	
	Second		+0.60	+1.0		+4.4	+5.0		+ 8.2	+18.1		+12.3	+18.8		
	Third		+0.70	+2.7		+6.4	+7.5		+10.2	+11.0		+13.0	+17.5		
	Wheat		Flag	+1.20	+1.8		+4.6	+8.1		+ 5.2	+12.5		+18.5	+24.0	
		Sonalika	Second	+2.60	+1.6		+4.8	+10.2		+10.2	+11.7		+19.4	+30.4	
			Third	+3.10	+4.8		+6.2	+9.6		+ 8.4	+17.3		+ 8.4	+20.0	
LSD at P = 0.05			0.09	0.32		0.94	0.76		1.36	1.82		2.42	1.76		

Table 8. Effect of gibberellic acid on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs.8 & 9.

Species	Cultivar	Leaf position	Days after anthesis											
			7			14			21			28		
			N	P		N	P		N	P		N	P	
Rice	Rasi	Flag	+1.2	+1.6		+3.2	+3.3		+3.2	+8.0	+7.2	+12.2		
		Second	+0.9	+2.0		+2.6	+3.6		+2.9	+6.0	+4.2	+14.2		
		Third	+1.2	+0.4		+2.0	+2.0		+0.8	+7.5	+4.7	+13.3		
	Kalojira	Flag	+2.1	+1.2		+2.4	+2.4		+2.4	+4.6	+4.5	+ 7.3		
		Second	+0.0	+0.9		+2.0	+2.1		+2.0	+4.2	+6.4	+ 8.6		
		Third	+0.6	+2.2		+3.6	+3.3		+4.8	+5.5	+8.3	+ 6.8		
Wheat	Sonalika	Flag	+1.2	+0.0		+2.4	+2.0		+2.8	+3.4	+4.1	+ 3.4		
		Second	+1.9	+1.8		+3.2	+2.4		+1.8	+2.8	+5.2	+ 5.8		
		Third	+2.3	+0.0		+1.6	+2.8		+6.2	+6.2	+3.5	+ 2.8		
LSD at P = 0.05			0.3	NS		0.63	0.69		0.95	1.03	1.11	1.32		

Table 9. Effect of abscisic acid on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control see Figs. 8 & 9.

Species	Cultivar	Leaf position	Days after anthesis											
			7			14			21			28		
			N	P		N	P		N	P		N	P	
Rice	Rasi	Flag	-1.25	-1.4	-3.5	-8.3	-5.6	-8.0	-11.5	-15.3				
		Second	-5.0	-2.4	-5.0	-8.2	-6.9	-7.2	-8.6	-13.0				
		Third	-6.0	-3.1	-0.86	-6.0	-3.5	-10.0	-6.1	-10.4				
	Kalojira	Flag	-1.6	-3.3	-8.4	-5.1	-4.8	-4.8	-9.4	-9.2				
		Second	-1.2	-1.2	-1.2	-6.0	-4.2	-10.0	-14.6	-6.8				
		Third	-0.6	-1.6	-4.6	-3.7	-4.5	-5.5	-5.2	-6.5				
	Wheat	Flag	-0.9	-3.3	-4.2	-4.1	-5.2	-7.5	-7.6	-11.3				
		Second	-0.42	-1.2	-3.2	-6.2	-4.6	-9.2	-12.0	-8.6				
		Third	-1.6	-2.6	-3.9	-4.7	-12.2	-6.3	-6.4	-5.0				
LSD at P = 0.05			0.31	0.23	0.63	1.49	0.89	1.62	1.6	2.13				

Table 10. Effect of (BA + GA₃) on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control see Figs. 8 & 9.

Species	Cultivar	Leaf position	Days after anthesis								
			7			14			21		
			N	P		N	P		N	P	
Rice	Rasi	Flag	+1.6	+2.7	+3.8	+8.5	+9.5	+19.9	+20.0	+44.0	
		Second	+1.8	+2.0	+1.6	+8.3	+14.2	+16.0	+10.0	+34.0	
		Third	+0.0	+3.6	+5.4	+8.0	+11.5	+24.0	+18.5	+38.0	
	Kalojira	Flag	+2.0	+1.2	+5.6	+6.6	+5.4	+9.4	+12.5	+19.0	
		Second	+1.2	+1.1	+5.5	+7.2	+6.1	+11.2	+13.3	+24.0	
		Third	+0.0	+3.2	+4.6	+7.7	+11.6	+19.3	+18.0	+23.0	
Wheat	Sonalika	Flag	+0.0	+1.9	+4.6	+8.7	+5.4	+12.5	+20.3	+26.0	
		Second	+2.4	+2.4	+6.2	+9.3	+11.0	+17.2	+22.0	+39.0	
		Third	+1.1	+2.3	+2.4	+4.7	+10.5	+16.6	+10.5	+15.0	
LSD at P = 0.05			0.016	0.22	0.94	1.72	1.03	2.33	2.56	3.62	

Table 11. Effect of benzyladenine on [³²P]-phosphate mobilization (M) from the fed-leaves to the grains and the retention capacity (R) of leaves in rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs.10 & 12.

Species	Cultivar	Leaf position	Days after anthesis											
			7			14			21			28		
			M	R		M	R		M	R		M	R	
Rice	Rasi	Flag	+8.7	+6.6		+9.4	+8.2		+7.5	+10.8		+6.0	+16.5	
		Second	+6.2	+2.5		+6.6	+4.2		+11.0	+8.4		+5.2	+13.5	
		Third	+2.4	+4.0		+5.0	+6.5		+4.0	+6.5		+0.9	+7.7	
	Kalojira	Flag	+16.8	+12.8		+11.1	+8.6		+6.4	+9.5		+8.6	+9.2	
		Second	+8.4	+2.6		+8.3	+14.0		+5.4	+14.2		+14.0	+12.2	
		Third	+2.3	+1.1		+3.2	+6.8		+3.2	+8.2		+3.0	+4.6	
Wheat	Sonalika	Flag	+12.0	+3.2		+15.0	+9.5		+12.0	+7.5		+9.0	+8.4	
		Second	+5.4	+2.6		+8.3	+11.5		+8.0	+12.8		+5.4	+11.7	
		Third	+3.3	+3.1		+6.0	+16.0		+4.6	+5.3		+3.2	+9.2	
LSD at P = 0.05			1.09	0.56		1.4	0.98		1.62	1.09		0.82	1.24	

Table 12. Effect of abscisic acid on [³²P]-phosphate mobilization (M) from the fed-leaves to the grains and the retention capacity (R) of leaves in rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 10 & 12.

Species	Cultivar	Leaf position	Days after anthesis											
			7		14		21		28					
			M	R	M	R	M	R	M	R				
Rice	Rasi	Flag	- 6.86	- 0.6	-13.6	- 2.4	- 4.9	- 6.6	- 6.6	-15.0				
		Second	- 8.96	- 0.64	-12.5	- 3.3	- 2.4	- 5.4	- 4.6	-14.4				
		Third	- 4.40	- 1.4	- 3.1	- 4.0	- 6.0	- 8.4	- 6.8	- 6.2				
	Kalojira	Flag	- 8.6	- 0.7	-17.5	-12.2	- 8.0	- 6.2	- 4.3	-14.6				
		Second	- 4.2	- 1.1	-15.3	- 8.2	- 6.0	- 5.4	- 2.6	-11.2				
		Third	- 2.8	- 2.4	- 3.2	- 6.5	- 3.4	- 3.2	- 3.5	- 5.5				
Wheat	Sonalika	Flag	-10.5	- 1.1	-16.7	- 4.0	- 4.6	- 2.9	- 7.4	-11.1				
		Second	- 4.7	- 0.9	- 7.6	- 6.5	- 6.8	- 3.6	- 5.4	-16.6				
		Third	- 5.7	- 1.2	- 2.7	- 4.2	- 3.8	- 4.4	- 2.1	- 5.0				
LSD at P = 0.05			0.69	0.04	2.21	0.82	1.33	0.84	0.24	0.72				

Table 13. Effects of hormones (BA and ABA) on RNA (R), histone protein (H) and RNA/histone ratio (R/H) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 15 & 16.

Species	Cultivar	Treat- ment	Leaf posi- tion	Days after anthesis											
				7			14			21			28		
				R	H	R/H	R	H	R/H	R	H	R/H	R	H	R/H
Rice	Rasi	BA	Flag	+4.6	-0.91	+6.2	+15.6	-2.5	+9.6	+29.6	-6.8	+15.5	+34.6	-10.2	+20.2
			2nd	+6.8	-0.42	+5.4	+23.0	-3.6	+12.0	+26.0	-7.3	+13.6	+32.3	-6.3	+22.5
			3rd	+3.8	-0.82	+5.0	+15.0	-4.8	+9.0	+14.7	-5.2	+8.5	+18.1	-4.6	+18.0
	ABA	Flag	-3.4	+0.44	-4.8	-8.1	+2.1	-8.4	-2.4	-4.5	-11.2	-13.7	+5.4	-24.0	
		2nd	-6.2	+0.36	-6.2	-3.8	+2.7	-6.2	-4.6	+5.4	-14.4	-11.7	+6.3	-22.0	
		3rd	-1.9	+0.82	-3.3	-7.5	+2.4	-7.5	-11.7	+7.2	-12.0	-9.0	+3.4	-14.2	
	Kalojira	Flag	+2.9	+0.0	+6.6	+5.2	-1.8	+7.3	+12.4	-4.8	+16.6	+15.7	-4.0	+24.0	
		2nd	+1.5	-1.7	+5.4	+4.34	-8.2	+8.4	+10.0	-7.6	+20.0	+20.5	-4.5	+18.6	
		3rd	+6.2	-0.8	+6.3	+4.8	-5.4	+6.4	+16.1	-6.4	+14.8	+27.2	-9.2	+16.0	
Wheat	ABA	Flag	-3.3	+1.9	-4.6	-7.8	+4.4	-6.9	-8.8	+2.1	-15.5	-10.1	+6.0	-17.0	
		2nd	-2.8	+0.0	-3.4	-3.7	+8.3	-5.5	-10.0	+9.3	-10.2	-12.2	+9.4	-15.8	
		3rd	-4.1	+0.6	-5.8	-12.1	+3.7	-8.2	-6.4	+4.9	-15.7	-9.4	+11.2	-13.3	
	BA	Flag	+2.3	-0.6	+3.8	+11.5	-10.4	+9.4	+13.0	-11.4	+10.3	+20.0	-13.6	+21.0	
		2nd	+3.7	-2.4	+5.4	+15.0	-3.6	+11.3	+16.0	-8.0	+15.5	+19.0	-9.5	+18.0	
		3rd	+3.0	-2.1	+6.2	+10.3	-5.8	+6.4	+22.0	-4.2	+14.5	+15.4	-8.2	+24.4	
	Sonalika	Flag	-5.0	+1.8	-4.6	-5.1	+4.5	-8.2	-6.8	+6.2	-16.4	-9.0	-8.0	-26.0	
		2nd	-2.4	+3.2	-4.9	-4.5	+8.5	-3.4	-5.7	+13.5	-17.2	-15.0	-6.7	-18.5	
		3rd	-4.6	+4.5	-3.3	-5.4	+12.0	-6.6	-9.0	+10.0	-12.0	-13.7	-9.6	-22.0	
LSD at P = 0.05				0.42	0.64	1.2	1.42	0.84	0.96	1.44	0.64	1.58	2.0	0.64	1.32

Table 14. Effects of hormones (BA and ABA) on free amino acid (AA) accumulation and protease activity (PA) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control see Figs. 17 & 18 .

Species	Cultivar	Treatment	Leaf position	Days after anthesis												
				7			14			21			28			
				AA	PA		AA	PA		AA	PA		AA	PA		
Rice	Rasi	BA	Flag	-6.0	-11.0		-10.0	- 8.3		-16.0	-18.0		-15.0	-20.6		
			Second	-8.6	- 2.0		- 4.0	- 6.6		- 9.4	-13.0		-10.5	-16.0		
			Third	-6.6	- 4.5		- 7.4	-17.0		- 8.4	-14.0		-10.7	-12.0		
		ABA	Flag	+4.7	+ 2.0		+ 6.0	+ 8.2		+ 9.4	+ 9.2		-14.4	+11.0		
			Second	+2.2	+ 3.2		+ 9.8	+ 5.4		+ 5.2	+ 6.5		-10.0	+ 5.0		
			Third	+3.3	+ 3.6		+ 8.2	+13.0		+ 7.5	+ 8.4		- 6.0	+ 4.5		
	Kalojira	BA	Flag	+1.6	-12.0		- 5.4	-18.2		-13.0	-13.0		-13.6	-20.0		
			Second	-2.4	- 6.0		- 4.8	-16.0		-16.0	-17.0		-11.5	-26.0		
			Third	-6.4	- 3.5		- 9.8	-12.2		-10.0	-16.0		-12.7	-19.5		
		ABA	Flag	+2.2	+ 6.2		+ 4.6	+ 8.2		+ 4.6	+ 8.2		- 9.4	+10.2		
			Second	+2.4	+ 3.8		+ 5.2	+10.3		+ 8.4	+12.6		-14.5	+13.3		
			Third	-2.5	+ 3.3		+ 5.7	+11.5		+ 5.1	+ 9.4		- 8.0	+ 6.6		
Wheat	Sonalika	BA	Flag	-3.7	- 3.5		- 6.6	-16.0		-11.5	- 9.5		-10.4	-10.5		
			Second	-2.0	- 3.2		-12.0	-12.5		-16.2	-16.0		-15.5	-16.5		
			Third	-7.5	- 4.6		- 9.3	-16.2		- 8.2	-13.0		-14.0	-16.0		
		ABA	Flag	+3.2	+ 6.2		+ 5.1	+ 4.6		+ 6.4	+ 8.0		- 2.9	+10.2		
			Second	+4.8	+ 4.2		+ 4.6	+10.2		+13.2	+11.0		- 4.8	+14.4		
			Third	+3.4	+ 7.0		+11.0	+ 8.5		+ 6.8	+ 7.6		- 6.6	+ 6.4		
	LSD at P = 0.05				NS	0.42		1.06	0.82		1.32	2.22		1.04	1.44	

Table 15. Effects of hormones (BA and ABA) on malondialdehyde (MDA) content and superoxide dismutase (SOD) activity in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig. 19.

Species	Cultivar	Treat- ment	Leaf position	Days after anthesis									
				7		14		21		28			
				MDA	SOD	MDA	SOD	MDA	SOD	MDA	SOD		
Rice	Rasi	BA	Flag	-0.8	+4.8	-2.4	+8.6	-7.22	+20.2	-18.5	+52.0		
			Second	-0.0	+6.4	-2.8	+11.0	-6.8	+16.5	-15.4	+44.0		
			Third	-1.6	+12.2	-4.6	+9.2	-11.0	+18.8	-16.2	+46.0		
		ABA	Flag	+0.0	-1.2	+1.6	-4.8	+5.4	-6.6	+11.0	-18.0		
			Second	+1.2	-1.6	+2.2	-2.4	+6.2	-9.3	+14.4	-15.3		
			Third	+3.1	-4.2	+4.6	-5.5	+8.4	-14.5	+9.5	-23.0		
		BA	Flag	-0.9	+6.2	-3.1	+6.8	-8.6	+14.4	-12.3	+36.0		
			Second	-1.8	+5.4	-2.4	+12.3	-9.5	+16.2	-18.5	+54.0		
			Third	-0.8	+5.9	-5.3	+13.5	-15.0	+18.0	-19.5	+41.0		
Wheat	Kalojira	ABA	Flag	+1.2	-2.4	+1.6	-4.6	+4.4	-8.5	+9.2	-16.6		
			Second	+0.6	-2.0	+2.2	-6.2	+6.2	-10.2	+11.0	-16.0		
			Third	+3.2	-3.4	+3.6	-5.2	+5.4	-13.5	+8.5	-19.0		
		BA	Flag	-0.8	+5.4	-2.6	+12.2	-8.2	+15.0	-13.0	+46.0		
			Second	-1.2	+6.6	-4.2	+9.0	-6.4	+12.0	-17.5	+54.0		
			Third	-1.9	+8.4	-6.6	+10.5	-10.0	+15.5	-14.5	+49.0		
	Sonalika	ABA	Flag	+0.9	-2.0	+1.4	-6.4	+5.5	-8.3	+9.6	-16.3		
			Second	+0.6	-1.6	+1.6	-5.5	+5.8	-10.5	+7.2	-18.6		
			Third	+1.2	-4.6	+3.4	-6.6	+8.9	-7.5	+12.5	-12.2		
LSD at P = 0.05				NS	0.84	1.24	1.19	1.09	1.42	1.16	2.28		

Table 16. Effects of hormones (BA and ABA) on the activity of catalase (Cata) and peroxidase (Pero) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig. 20.

Species	Cultivar	Treat- ment	Leaf position	Days after anthesis								
				7		14		21		28		
				Cata	Pero	Cata	Pero	Cata	Pero			
Rice	Rasi	BA	Flag	+6.0	+6.0	+8.6	+22.0	+13.3	+18.2	+52.0	+19.3	
			Second	-2.3	+5.5	+7.0	+14.0	+11.2	+14.5	+38.0	+13.6	
			Third	+10.2	+3.2	+13.4	+8.4	+24.5	+15.0	+28.0	+12.2	
		ABA	Flag	+2.0	+4.2	-7.2	-9.0	-10.0	-12.3	-16.0	-8.0	
			Second	-6.9	-5.1	-5.5	-6.0	-6.4	-6.8	-15.0	-10.2	
			Third	-4.6	-4.0	-4.3	-8.2	-20.0	-15.0	-28.0	-16.0	
	Kalojira	BA	Flag	-2.2	+11.0	+5.2	+22.0	+14.0	+15.4	+25.0	+6.2	
			Second	+2.4	+14.0	+5.5	+12.0	+18.0	+20.0	+33.0	+15.0	
			Third	+4.5	+8.3	+7.2	+16.0	+16.0	+14.0	+50.0	+10.4	
		ABA	Flag	-2.4	-4.2	-4.9	-5.9	-8.5	-4.6	-13.4	-7.2	
			Second	-4.4	-2.6	-6.2	-6.2	-10.2	-12.4	-16.5	-18.2	
			Third	-6.2	-6.2	-6.5	-10.0	-10.5	-11.5	-10.0	-8.5	
Wheat	Sonaliika	BA	Flag	+2.7	+6.2	+10.3	+12.0	+22.0	+16.5	+45.0	+26.0	
			Second	-2.4	+3.6	+16.0	+10.0	+24.0	+18.7	+44.0	+24.0	
			Third	+5.3	+6.6	+14.0	+14.0	+30.0	+9.6	+36.0	+20.0	
		ABA	Flag	-2.0	-4.2	-6.6	-8.4	-5.5	-7.6	-16.0	-8.0	
			Second	-0.0	-3.1	-6.0	-12.2	-10.5	-10.2	-12.0	-15.4	
			Third	-3.5	-8.4	-10.0	-6.8	-5.5	-8.3	-13.0	-7.8	
	LSD at P = 0.05				0.62	NS	0.46	1.84	1.62	1.24	2.06	1.48

Table 17. Changes in the rate of transpiration ($\text{mg.cm}^{-2}.\text{h}^{-1}$) by the whole plant and the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. The leaves whose transpiration rate not being measured, were smeared with vaseline on both sides.

Species	Cultivar	Transpiration by	Days after anthesis				
			0	7	14	21	28
Rice	Rasi	Total plant	18.2	17.8	16.0	13.6	7.4
		Only flag leaf	24.5	23.9	21.0	16.4	10.8
		Only second leaf	23.0	23.4	20.0	15.8	12.6
		Only third leaf	21.0	20.0	16.2	12.0	6.4
	Kalojira	Total plant	14.0	13.4	12.8	9.6	6.8
		Only flag leaf	21.2	21.0	18.4	14.5	9.9
		Only second leaf	20.0	20.5	18.0	14.4	8.4
		Only third leaf	17.6	16.4	13.4	11.2	6.0
Wheat	Sonalika	Total plant	12.2	12.6	11.0	9.2	5.8
		Only flag leaf	18.0	18.4	16.0	14.4	9.5
		Only second leaf	19.6	19.0	17.3	13.7	8.6
		Only third leaf	17.0	15.4	12.2	8.5	5.4
	LSD at P = 0.05		0.74	0.58	1.46	0.42	0.59

Table 18. Effects of hormones (BA and ABA) on the rate of transpiration by rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Table 17.

Species	Cultivar	Transpiration by	Days after anthesis							
			BA				ABA			
			7	14	21	28	7	14	21	28
Rice	Rasi	Total plant	+2.4	+3.2	+16.2	+24.4	-0.8	-4.4	-8.2	-14.3
		Flag leaf	+3.4	+4.6	+13.3	+16.0	-2.1	-3.3	-5.8	-11.2
		Second leaf	+4.9	+6.7	+12.0	+20.0	-0.9	-2.5	-6.4	- 9.5
		Third leaf	+8.4	+6.8	+15.0	+ 8.5	-2.4	-6.6	-10.0	- 8.5
	Kelotira	Total plant	+0.9	+4.5	+ 8.2	+21.5	-0.8	-4.2	-8.4	-10.8
		Flag leaf	+1.8	+3.8	+ 9.4	+22.6	-0.6	-3.1	-7.2	-13.3
		Second leaf	+2.4	+5.4	+ 7.5	+26.4	-1.2	-3.6	-6.8	-12.3
		Third leaf	-3.1	-6.0	+10.0	+10.2	-1.8	-5.2	-10.6	- 9.5
Wheat	Sonaliika	Total plant	+1.6	+3.6	+11.4	+16.0	-2.2	-3.6	-8.5	-10.6
		Flag leaf	+0.9	+6.5	+12.2	+18.4	-0.9	-1.2	-5.2	-12.4
		Second leaf	+1.9	+5.2	+ 9.5	+15.2	-1.2	-2.2	-6.5	-12.5
		Third leaf	+3.2	+6.1	+ 6.4	+ 9.5	-2.6	-6.2	-9.2	-12.8
	LSD at P = 0.05		0.06	0.41	0.76	1.03	0.06	0.32	0.87	0.56

Table 19. Effects of hormones (BA and ABA) on proline accumulation in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig. 21.

Species	Cultivar	Leaf position	Days after anthesis									
			BA					ABA				
			7	14	21	28	7	14	21	28		
Rice	Rasi	Flag	-2.1	-5.5	-11.2	-13.4	+4.3	+7.4	+12.5	+9.4		
		Second	-4.1	-10.1	- 7.3	- 8.2	+2.0	+6.0	+ 8.4	+8.4		
		Third	+0.0	-6.9	-15.0	- 5.8	+6.4	+2.7	+ 8.9	+7.8		
	Kalojira	Flag	-9.5	-3.7	-11.4	- 8.2	+4.5	+11.0	+ 9.2	+6.4		
		Second	-3.9	-11.6	- 9.7	-12.8	+1.9	+6.0	+10.2	+9.5		
		Third	-3.5	-10.1	- 3.2	- 6.8	+5.7	+6.7	+16.4	+9.6		
Wheat	Sonaliika	Flag	-4.5	-5.1	- 9.7	-10.4	+2.2	+8.6	+ 6.0	+13.3		
		Second	-2.1	-4.4	- 8.0	-13.6	+4.2	+4.4	+8.4	-17.4		
		Third	-0.3	-7.2	- 6.1	-11.0	+4.9	+5.7	+13.3	+9.0		
	LSD at P = 0.05		0.46	0.76	1.84	0.64	0.16	0.36	0.89	1.06		

Table 20. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein (Prot) contents ($\text{mg.g}^{-1}\text{F.W.}$) in the flag, second and third leaf of rice (cv. Rasi) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

Treatment	Leaf position	Days after anthesis								
		7			14			21		
		Chl.	Prot.		Chl.	Prot.		Chl.	Prot.	
Control	Flag	1.22	71.0		0.79	60.0		0.34	49.0	
	Second	0.36	62.0		0.71	56.0		0.36	46.0	
	Third	0.72	59.5		0.52	50.0		0.16	40.5	
Panicle removed at 0 DAA (anthesis stage)	Flag	1.16(-4.9)	72.0(+1.4)		0.93(+18)	62.0(+3.3)		0.43(+26)	58.2(+16)	
	Second	0.38(+2.0)	63.4(+2.2)		0.74(-5)	58.0(-3.4)		0.46(+27)	54.5(+17)	
	Third	0.73(+2.7)	60.5(+3.4)		0.54(+3)	52.2(-4.0)		0.19(+18)	44.5(+10)	
Panicle removed at 7 DAA (grain filling stage)	Flag	-	-		0.78(+1.2)	60.5(-0.3)		0.42(+23)	55.5(+12)	
	Second	-	-		0.73(+2.8)	60.6(+8.2)		0.44(+22)	51.0(+12)	
	Third	-	-		0.53(+2.0)	52.3(+4.6)		0.19(+18)	45.3(+12)	
Panicle removed at 14 DAA (grain development stage)	Flag	-	-		-	-		0.35(+2.9)	50.2(+2.0)	
	Second	-	-		-	-		0.36(+0)	47.2(-2.5)	
	Third	-	-		-	-		0.15(-6.0)	40.0(-2.8)	
Panicle removed at 21 DAA (grain maturation stage)	Flag	-	-		-	-		-	-	
	Second	-	-		-	-		-	-	
	Third	-	-		-	-		-	-	
LSD at P = 0.05		0.0082	0.86		0.0039	1.2		0.0046	1.54	
								0.0094	1.33	

Table 21. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} , F.W.) in the flag, second and third leaf of rice plant (cv. Kalojira) during the progress of reproductive development. Figures within parentheses indicate percentage increase (-) or decrease (-) over control.

Treatment	Leaf position	Days after anthesis					
		7		14		21	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
Control	Flag	1.04	82.0	0.78	68.0	0.54	59.0
	Second	0.96	76.0	0.72	64.0	0.46	54.0
	Third	0.74	62.5	0.53	55.0	0.26	46.0
Panicle removed at 0 DAA (anthesis stage)	Flag	1.03(-0.9)	83.4(+1.7)	0.81(+3.8)	71.0(+4.4)	0.59(+9.2)	64.0(+8.4)
	Second	0.98(+2.0)	76.0(+0)	0.74(+2.7)	66.0(+3.1)	0.51(+10)	58.0(+7.4)
	Third	0.74(+0)	60.6(-3.6)	0.56(+5.6)	56.5(+3.0)	0.21(-11.5)	50.4(-9.5)
Panicle removed at 7 DAA (grain filling stage)	Flag	-	-	0.77(-1.2)	69.0(+1.6)	0.57(+5.5)	62.4(+5.7)
	Second	-	-	0.74(+2.7)	66.0(+3.1)	0.52(+13)	58.5(-7.4)
	Third	-	-	0.56(+5.6)	57.0(+3.6)	0.28(+7.6)	48.8(+6.0)
Panicle removed at 14 DAA (grain devert. stage)	Flag	-	-	-	-	0.53(-1.8)	58.0(+1.8)
	Second	-	-	-	-	0.48(+4.3)	55.2(-1.9)
	Third	-	-	-	-	0.27(+4.2)	45.0(-2.6)
Panicle removed at 21 DAA (grain maturation stage)	Flag	-	-	-	-	-	-
	Second	-	-	-	-	-	-
	Third	-	-	-	-	-	-
LSD at $P = 0.05$		NS	0.36	0.005	0.27	0.008	1.24
						0.006	1.68

Table 22. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} , F.W.) in the flag, second and third leaf of wheat plant (cv. Sonalika) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

Treatment	Leaf position	Days after anthesis					
		7		14		21	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
Control	Flag	1.01	68.0	0.74	56.0	0.53	48.0
	Second	0.92	61.0	0.63	51.0	0.44	43.0
	Third	0.74	54.0	0.51	47.0	0.21	49.0
Panicle removed at 0 DAA (anthesis stage)	Flag	1.09(+8.1)	72.2(+6.1)	0.76(+2.7)	58.0(+3.5)	0.59(+11.3)	52.0(+8.4)
	Second	0.93(-1.0)	63.0(+3.2)	0.65(+3.1)	54.0(+5.8)	0.47(+6.8)	48.0(+11.6)
	Third	0.76(-2.7)	54.5(+1.2)	0.53(+4.0)	50.0(+6.4)	0.26(-23)	41.1(+5.3)
Panicle removed at 7 DAA (grain filling stage)	Flag	-	-	0.73(-1.3)	57.0(+1.8)	0.56(+5.6)	49.5(+2.4)
	Second	-	-	0.64(+1.5)	54.0(+5.8)	0.43(+2.3)	44.0(+2.6)
	Third	-	-	0.52(+2.0)	56.5(-1.0)	0.24(+8.5)	40.5(+3.6)
Panicle removed at 14 DAA (grain devet. stage)	Flag	-	-	-	-	0.53(+0)	49.0(+2.2)
	Second	-	-	-	-	0.45(+2.3)	42.6(-1.6)
	Third	-	-	-	-	0.23(+8.6)	38.5(-1.8)
Panicle removed at 21 DAA (grain maturation stage)	Flag	-	-	-	-	-	0.20(+0)
	Second	-	-	-	-	-	0.13(+8)
	Third	-	-	-	-	-	0.04(+0)
LSD at P = 0.05		0.0033	0.62	0.0041	0.94	0.0068	1.20
							0.0051
							1.06

Table 23. Effect of panicle removal at different reproductive stages on changes in nitrogen and phosphorus contents (mg.g⁻¹.D.W.) in the flag, second and third leaf of rice plant (cv. Rasi) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control

Treatment	Leaf position	Days after anthesis								
		7			14			21		
		Nitrogen	Phosphorus		Nitrogen	Phosphorus		Nitrogen	Phosphorus	
Control	Flag	30.8	7.2	28.0	6.5	25.2	5.2	18.5	3.4	
	Second	32.3	7.4	29.2	6.1	26.0	5.8	20.2	4.4	
	Third	25.1	6.3	22.5	5.6	21.6	3.6	16.4	2.5	
Panicle removed at 0 DAA (anthesis stage)	Flag	32.7(+6.0)	7.4(+2.7)	29.1(+4.0)	7.2(+10.7)	28.0(+12.8)	6.08(+17)	24.6(+30.6)	5.2(+52)	
	Second	33.0(+2.7)	7.4(+0)	30.5(+4.1)	6.7(+9.8)	28.4(+9.2)	6.49(+18.4)	24.0(+20)	5.0(+13)	
	Third	25.5(+1.2)	6.5(+3.1)	24.2(+7.7)	5.4(+3.5)	24.3(+4.7)	3.68(+2.2)	18.2(+13)	3.15(+26)	
Panicle removed at 7 DAA (grain filling stage)	Flag	-	-	28.7(+2.5)	6.7(+3.0)	27.0(+7.2)	6.13(+13)	23.6(+26)	4.3(+44)	
	Second	-	-	30.3(+3.7)	6.2(+1.3)	29.1(+11.9)	6.22(+7.2)	23.0(+15)	5.0(+22)	
	Third	-	-	23.9(+6.3)	5.32(+5.3)	23.9(+10.9)	3.96(+10)	17.8(+8.5)	2.7(+8)	
Panicle removed at 14 DAA (grain development stage)	Flag	-	-	-	-	25.9(+3.1)	5.44(+4.8)	18.8(+1.6)	3.5(+2.9)	
	Second	-	-	-	-	26.6(+2.2)	5.72(+3.1)	21.5(+7.5)	4.3(+2.2)	
	Third	-	-	-	-	21.6(+1.6)	3.67(+1.2)	17.0(+3.7)	2.6(+4.0)	
Panicle removed at 21 DAA (grain maturation stage)	Flag	-	-	-	-	-	-	17.3(+3.3)	3.5(+2.9)	
	Second	-	-	-	-	-	-	21.0(+5.0)	4.4(+0)	
	Third	-	-	-	-	-	-	16.0(+2.5)	2.6(+4)	
LSD at P = 0.05		C.21	NS	0.06	0.08	0.69	0.22	C.86	0.34	

Treatment	Leaf position	Days after anthesis											
		7			14			21			28		
		Nitrogen	Phosphorus		Nitrogen	Phosphorus		Nitrogen	Phosphorus		Nitrogen	Phosphorus	
Control	Flag	31.0	6.8		28.5	5.8		26.0	5.2		21.0	4.1	
	Second	30.0	6.5		28.0	5.6		25.4	4.7		19.4	3.5	
	Third	25.5	5.6		22.1	4.8		19.0	3.8		16.5	2.8	
Panicle removed at 0 DAA (anthesis stage)	Flag	31.8(+2.5)	7.7(+4.4)		30.2(+6.0)	6.3(+8.6)		28.6(+9.0)	6.03(+15.3)		23.0(+9.5)	5.2(+26.8)	
	Second	30.3(+1.0)	6.8(+4.6)		31.1(+11)	6.2(+10.7)		28.0(+13)	5.4(+14.8)		22.2(+14.4)	4.6(+31)	
	Third	25.7(+0.8)	5.8(+4.0)		24.6(+11.3)	5.0(+8.3)		20.7(+8.9)	4.7(+23)		18.6(+15)	3.4(+21)	
Panicle removed at 7 DAA (grain filling stage)	Flag				29.6(+3.8)	5.9(+1.7)		28.8(+10.7)	5.8(+11.5)		23.3(+10.9)	5.0(+21.9)	
	Second	-	-		28.5(+1.7)	5.7(+1.8)		27.0(+9.4)	5.5(+17)		22.5(+16)	4.3(+22.8)	
	Third				23.0(+4.0)	5.0(+0)		20.0(+5.4)	4.4(+17)		17.8(+7.8)	3.4(+21)	
Panicle removed at 14 DAA (grain devert. stage)	Flag							26.8(+3.0)	5.3(+2.2)		21.8(+3.8)	4.3(+9)	
	Second	-	-		-	-		25.3(+0.8)	4.5(+1.8)		19.4(+0)	3.3(+5.7)	
	Third							18.6(-2.1)	3.9(+3.1)		16.6(+0.8)	2.6(+7.1)	
Panicle removed at 21 DAA (grain maturation stage)	Flag										21.6(+3.0)	4.3(+4.8)	
	Second	-	-		-	-		-	-		19.5(+1.5)	3.6(+2.8)	
	Third										16.7(+0.8)	2.9(+3.5)	
LSD at P = 0.05		0.06	0.11		0.36	0.09		0.56	0.09		0.34	0.47	

Table 25. Effect of panicle removal at different reproductive stages on changes in nitrogen and phosphorus contents ($\text{mg} \cdot \text{g}^{-1} \cdot \text{D.W.}$) in the flag, second and third leaf of wheat plant (cv. Sonalika) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

Treatment	Leaf position	Days after anthesis											
		7			14			21			28		
		Nitrogen	Phosphorus		Nitrogen	Phosphorus		Nitrogen	Phosphorus		Nitrogen	Phosphorus	
Control	Flag	26.5	6.0		24.4	5.1		22.2	3.9		16.8	3.0	
	Second	25.1	5.6		23.5	4.8		19.5	3.4		15.2	2.6	
	Third	23.0	4.8		18.5	4.1		16.0	3.0		14.0	2.0	
Panicle removed at 0 DAA (anthesis stage)	Flag	26.9(+1.6)	6.2(+3.3)		25.3(+3.6)	5.8(+13.7)		24.1(+9)	4.5(+15.3)		18.9(+12.5)	3.66(+22.3)	
	Second	25.4(+1.1)	5.2(+7.1)		24.2(+2.9)	5.4(+12.5)		20.5(+5.2)	4.1(+20.5)		16.8(+11)	3.10(+19.7)	
	Third	23.6(+2.6)	4.6(-4.1)		18.8(+1.6)	4.3(+4.6)		16.6(+3.6)	3.6(+20)		14.8(+5.7)	2.5(+20)	
Panicle removed at 7 DAA (grain filling stage)	Flag				25.1(+1.6)	5.11(+1.0)		22.8(+2.7)	4.1(+5.0)		17.8(+6.3)	3.3(+10)	
	Second	-	-		24.0(+2.1)	4.9(+2.0)		20.3(+4.2)	3.6(+5.3)		15.5(+1.9)	2.9(+13.6)	
	Third				18.9(+2.1)	4.2(+2.4)		16.8(+5.0)	3.4(+10)		14.8(+5.0)	2.3(+15)	
Panicle removed at 14 DAA (grain devert. stage)	Flag							22.2(+0.4)	3.8(-3.3)		17.2(+2.3)	3.1(+3.1)	
	Second	-	-		-	-		19.3(-1.0)	3.6(+5.8)		15.4(+1.3)	2.6(+0)	
	Third							16.2(-2.5)	3.0(+0)		13.8(-1.4)	2.0(+0)	
Panicle removed at 21 DAA (grain maturation stage)	Flag										16.6(-1.1)	2.9(-3.0)	
	Second	-	-		-	-		-	-		15.4(+1.3)	2.6(+7.6)	
	Third										14.0(+0)	2.0(+3)	
LSD at P = 0.05		NS	0.045		0.015	0.01		0.16	0.21		0.49	0.23	

Table 26. Effect of panicle removal at different reproductive stages on [³²P]-phosphate retention by fed leaves (KBq. Leaf⁻¹.h⁻¹) and stem (when fed through the flag leaf, KBq.g⁻¹.F.W.h⁻¹) of rice plant (cv. Rasi) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

Treatment	Leaf position	Days after anthesis			
		7	14	21	28
Control	Flag	350	262	229	158
	Second	340	241	245	190
	Third	270	208	179	108
	Stem	72	75	73	62
Panicle removed at 0 DAA (anthesis stage)	Flag	320(-8.5)	295(+12.5)	254(+11.0)	220(+39)
	Second	310(-8.8)	283(+17.0)	262(+7.0)	210(+10)
	Third	275(+1.8)	229(10)	204(+18)	33(+25)
	Stem	75(+4.0)	82(+9)	80(+10)	75(+21)
Panicle removed at 7 DAA (grain filling stage)	Flag	-	258(+1.5)	250(+9.0)	210(+33)
	Second	-	245(+1.6)	258(+5.8)	204(+7)
	Third	-	220(+1.6)	208(+16)	125(+15)
	Stem	-	80(+6.6)	78(+7)	70(+12)
Panicle removed at 14 DAA (grain deve- lopment stage)	Flag	-	-	233(+1.7)	162(+2.5)
	Second	-	-	241(-1.6)	195(+2.6)
	Third	-	-	287(+4.4)	116(+7.4)
	Stem	-	-	71(-2.7)	64(+3.0)
Panicle removed at 21 DAA (grain maturation stage)	Flag	-	-	-	155(-1.8)
	Second	-	-	-	204(+7.3)
	Third	-	-	-	118(+9.2)
	Stem	-	-	-	63(+1.6)
LSD at P = 0.05		4.36	2.37	3.20	5.84

Table 27. Effect of panicle removal at different reproductive stages on [³²P]-phosphate retention by the fed leaves (KBq. Leaf⁻¹.h⁻¹) and stem (when fed through the flag leaf, KBq.g⁻¹.F.W.h⁻¹) of rice plant (cv. Kalojirra) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

Treatment.	Leaf position	Days after anthesis			
		7	14	21	28
Control	Flag	352	316	270	200
	Second	395	308	225	183
	Third	308	266	189	133
	Stem	68	70	72	65
Panicle removed at 0 DAA (anthesis stage)	Flag	333(-5.3)	329(+4.1)	283(+4.8)	233(+16)
	Second	354(-10)	325(+5.5)	241(+7.4)	216(+18)
	Third	316(-2.5)	283(+6.2)	208(+10)	158(+18)
	Stem	70(+3.0)	73(+4.2)	78(+8)	74(+13)
Panicle removed at 7 DAA (grain filling stage)	Flag	-	310(-1.8)	287(+6.2)	229(+14)
	Second	-	295(-4.0)	250(+10)	208(+13)
	Third	-	270(+1.5)	200(+5.8)	154(+15)
	Stem	-	69(+1.4)	76(+5.5)	71(+9)
Panicle removed at 14 DAA (grain development stage)	Flag	-	-	258(+4.4)	204(+2.0)
	Second	-	-	225(+0)	179(+2.4)
	Third	-	-	183(-3.1)	129(+3)
	Stem	-	-	73(+1.3)	66(+3)
Panicle removed at 21 DAA (grain maturation stage)	Flag	-	-	-	195(+2.5)
	Second	-	-	-	191(+4.3)
	Third	-	-	-	137(+3.0)
	Stem	-	-	-	62(-4.6)
LSD at P = 0.05		3.22	4.1	3.2	5.8

Table 28. Effect of panicle removal at different reproductive stages on [³²P]-phosphate retention by the fed leaves (KBq. Leaf⁻¹.h⁻¹) and stem (when fed through the flag leaf, KBq.g⁻¹.F.W.h⁻¹) of wheat plant (cv. Sonalika) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

Treatment	Leaf position	Days after anthesis			
		7	14	21	28
Control	Flag	258	245	208	125
	Second	266	233	191	108
	Third	254	204	137	87
	Stem	64	65	63	60
Panicle removed at 0 DAA (anthesis stage)	Flag	251(-2.7)	258(+5.0)	220(+5.7)	138(+10)
	Second	258(-3.6)	241(+3.4)	204(+6.8)	125(+15)
	Third	250(-1.5)	210(+3.0)	150(+9.4)	95(+9)
	Stem	66(+3.0)	69(+6.0)	66(+4.7)	70(+14)
Panicle removed at 7 DAA (grain filling stage)	Flag	-	233(-4.9)	225(+8.0)	136(+9.8)
	Second	-	225(-3.4)	200(+4.7)	116(+7.4)
	Third	-	205(+0.4)	154(+12)	95(+9)
	Stem	-	67(+3)	67(+6.3)	68(+13)
Panicle removed at 14 DAA (grain development stage)	Flag	-	-	212(-19)	127(+1.6)
	Second	-	-	187(-2.0)	105(+2.7)
	Third	-	-	133(+3.0)	83(-4.5)
	Stem	-	-	64(+1.5)	62(+3.3)
Panicle removed at 21 DAA (grain maturation stage)	Flag	-	-	-	125(-0)
	Second	-	-	-	104(-3.7)
	Third	-	-	-	85(-2.2)
	Stem	-	-	-	63(+5)
LSD at P = 0.05		2.1	2.53	3.32	4.8

Table 29. Effect of leaf removal on chlorophyll (Chl) and protein (Prot) contents of the remaining leaves of rice plant (cv. Rasi) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 1 & 2.

Treatment	Leaf position	Days after anthesis							
		7		14		21		28	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
Removal of :									
Flag leaf	Second	+4.2	+5.5	-8.5	-8.4	-13.7	-10.2	-38.0	-14.5
	Third	+3.7	+2.8	-1.8	-2.4	-2.7	-2.8	-10.0	-3.1
Second leaf	Flag	+6.84	+3.4	-5.0	-6.4	-12.3	-8.2	-24.0	-10.6
	Third	+1.2	+0.8	-3.2	-2.1	-11.0	-1.6	-8.8	-4.2
Third leaf	Flag	+0.8	+1.4	-1.6	-1.2	-2.4	-2.6	-4.8	-1.4
	Second	+2.5	+1.2	-1.2	-1.6	-4.2	-1.8	-3.4	-2.4
LSD at P = 0.05		0.32	0.22	0.34	0.64	0.42	0.23	1.84	1.06

Table 30. Effect of leaf removal on chlorophyll (Chl) and protein (Prot) content of the remaining leaves of rice plant (cv. Kalojira) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 1 & 2.

Treatment	Leaf position	Days after anthesis							
		7		14		21		28	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
Removal of :									
Flag leaf	Second	+5.1	+5.3	-4.1	-12.0	-12.5	-13.2	-36.0	-16.0
	Thirld	+4.6	+2.1	-3.1	-2.6	-4.2	-3.1	-12.0	-3.4
Second leaf	Flag	+4.6	+7.2	-5.8	-5.2	-18.0	-7.5	-22.5	-8.9
	Thirld	+2.3	+1.6	-2.6	-2.4	-6.1	-2.6	-6.3	-4.6
Thirld leaf	Flag	+2.6	+1.2	-2.1	-1.9	-8.6	-2.1	-3.1	-4.5
	Second	+2.3	+1.4	-1.6	-3.1	-3.8	-3.4	-4.2	-1.8
LSD at P = 0.05		0.21	0.14	0.08	0.67	1.87	1.03	1.63	1.77

Table 31. Effect of leaf removal on chlorophyll (Chl) and protein (Prot) contents of the remaining leaves of wheat plant (cv. Sonalika) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig.3.

Treatment	Leaf position	Days after anthesis							
		7		14		21		28	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
Removal of : Flag leaf	Second	+3.1	+3.8	-5.5	-7.4	-7.5	-8.5	-18.0	-8.2
	Third	+1.3	+1.4	-2.1	-2.4	-1.6	-2.8	-4.3	-2.8
Second leaf	Flag	+4.8	+1.8	-3.4	-3.8	-8.8	-4.2	-10.3	-3.4
	Third	+3.2	+1.2	+1.2	-2.1	-2.3	-1.4	-2.8	-1.6
Third leaf	Flag	+2.6	+0.96	+1.6	-0.8	-1.6	-3.4	-3.1	+2.8
	Second	+1.8	+1.21	-2.4	-1.5	-2.6	-1.8	-3.5	-1.6
LSD at P = 0.05		0.16	0.32	0.11	0.08	0.28	0.64	1.44	1.06

Table 32. Effect of leaf removal on nitrogen (N) and phosphorus (P) contents of the remaining leaves of rice plant (cv. Rasi) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 8 & 9.

Treatment	Leaf position	Days after anthesis							
		7		14		21		28	
		N	P	N	P	N	P	N	P
Removal of :									
Flag leaf	Second	+3.6	-9.4	-5.4	-9.3	-8.0	-14.2	-15.4	-26.2
	Third	+0.36	-1.5	-1.3	-2.0	-0.95	- 5.2	- 2.4	- 8.4
Second leaf	Flag	+2.4	-5.4	-3.1	-4.2	-6.2	-7.6	-8.2	-14.2
	Third	+0.48	-1.8	-0.6	-0.9	-2.6	-2.2	-1.2	- 3.6
Third leaf	Flag	+0.32	-1.3	-0.8	-2.2	-1.2	-3.7	-1.0	- 4.6
	Second	-0.21	-0.9	-1.2	-1.1	-1.6	-1.2	-1.3	- 2.1
LSD at P = 0.05		0.06	0.03	0.13	0.41	0.062	1.21	1.06	1.84

Table 33. Effect of leaf removal on nitrogen (N) and phosphorus (P) contents of the remaining leaves of rice plant (cv. Kalojira) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 8 & 9 .

Treatment	Leaf position	Days after anthesis							
		7		14		21		28	
		N	P	N	P	N	P	N	P
Removal of :									
Flag leaf	Second	+3.5	-10.6	-6.6	-8.7	-8.0	-16.0	-9.3	-21.0
	Third	+0.9	- 3.4	-2.1	-4.4	-2.8	- 5.2	-2.1	- 7.4
Second leaf	Flag	+1.6	-6.0	-2.2	-4.2	-4.6	-18.0	-5.4	-18.5
	Third	+1.9	-2.7	-1.6	-3.2	-3.0	-12.4	-1.4	- 6.8
Third leaf	Flag	+2.6	+2.0	-1.6	-1.2	-2.9	-2.0	-1.3	- 3.1
	Second	+1.4	-2.8	-1.42	-2.8	-1.2	-2.4	-1.8	- 4.6
LSD at P = 0.05		0.04	0.32	0.21	0.36	0.22	1.08	0.67	1.63

Table 34. Effect of leaf removal on nitrogen (N) and phosphorus (P) contents of the remaining leaves of wheat plant (cv. Sonalika) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs.8 & 9.

Treatment	Leaf position	Days after anthesis											
		7			14			21			28		
		N	P		N	P		N	P		N	P	
Removed of :													
Flag leaf	Second	+3.4	-3.7		-3.3	-12.8		-8.2	-14.0		-10.6	-16.5	
	Thirđ	+0.86	-4.2		-1.6	- 5.0		-2.64	- 2.8		- 3.4	- 6.0	
Second leaf	Flag	+2.6	-3.4		-1.8	-4.0		-1.2	-4.2		-8.5	-8.7	
	Thirđ	+0.8	-4.3		-1.1	-5.8		-2.4	-2.1		-2.3	-3.9	
Thirđ leaf	Flag	-1.8	-1.7		-1.85	-2.0		-0.9	-2.2		-2.2	-3.8	
	Second	-0.4	-0.6		-0.86	-2.1		-0.85	-1.8		-2.6	-2.4	
LSD at P = 0.05		0.04	0.12		0.06	0.21		0.16	0.20		0.35	0.87	

Table 35. Effect of leaf removal on [^{32}P]-phosphate mobilization from the remaining leaves to the grains of rice plant (cv. Rasi) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig.10.

Treatment	Leaf position	Days after anthesis			
		7	14	21	28
Removal of :					
Flag leaf	Second	+19.2	+35.0	+10.0	+8.4
	Third	+ 9.3	+ 9.0	+ 8.4	+2.9
Second leaf	Flag	+16.3	+13.0	+8.0	+4.2
	Third	+ 4.3	+ 6.0	+4.1	+1.4
Third leaf	Flag	+ 2.2	+2.6	+2.2	+5.5
	Second	+ 3.2	+4.2	+3.4	+2.7
LSD at P = 0.05		1.72	2.30	1.51	0.73

Table 36. Effect of leaf removal on [^{32}P]-phosphate mobilization from the remaining leaves to the grains of rice plant (cv. Kalojira) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig.10.

Treatment	Leaf position	Days after anthesis			
		7	14	21	28
Removal of :					
Flag leaf	Second	+18.4	+30.6	+11.5	+4.2
	Third	+ 6.7	+11.2	+ 7.8	+2.6
Second leaf	Flag	+10.8	+14.2	+4.3	+4.3
	Third	+ 3.3	+ 2.4	+3.9	+3.2
Third leaf	Flag	+ 5.8	+ 4.8	+1.7	+4.3
	Second	+ 3.2	+ 3.2	+3.2	+3.7
LSD at P = 0.05		1.84	2.64	0.62	0.33

Table 37. Effect of leaf removal on [^{32}P]-phosphate mobilization from the remaining leaves to the grains of wheat plant (cv. Sonalika) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig.10.

Treatment	Leaf position	Days after anthesis			
		7	14	21	28
Removal of :					
Flag leaf	Second	+15.3	+19.7	+12.0	+6.8
	Third	+ 7.9	+ 7.2	+ 7.0	+4.7
Second leaf	Flag	+ 8.2	+ 8.4	+ 6.8	+4.9
	Third	+ 4.0	+ 4.0	+ 2.4	+2.6
Third leaf	Flag	+ 1.1	+ 1.2	+ 1.8	+2.4
	Second	+ 2.1	+ 1.6	+ 3.4	+3.7
LSD at P = 0.05		1.59	0.82	1.53	0.44

Table 38. Effect of spikelet removal on branch production, leaf area and longevity of the whole plant of rice (cv. Rasi). P = Presence of branch production, A = absence of branch production

Treatment	Main tiller (MT)					Secondary branch (SB)					Tertiary branch (TB)				
	Branch production	Leaf area (cm ²)			Longevity of MT (d)	Branch production	Leaf area (cm ²)			Longevity of MT + SB (d)	Branch production	Leaf area (cm ²)			Total longevity of (MT+SB+TB) (d)
		Flag	Second				Flag	Second				Flag	Second		
Control (Intact)	A	28	39		126	A	18	19		147	A	13	14		166
Removal of :															
25% Spikelets	A	28	39		126	A	18	19		147	A	13	14		166
50% Spikelets	P	28	39		126	A	18	19		147	A	13	14		166
75% Spikelets	P	28	39		129	P	18	19		149	A	13	14		166
100% Spikelets	P	28	39		133	P	18	19		154	A	13	14		173
Emasculated	P	28	39		133	P	18	19		154	A	13	14		173
Second leaf + 100% Spikelets	A	-	-		-	A	-	-		-	A	-	-		-

Table 39. Effect of spikelet removal on branch production, leaf area and longevity of the whole plant of rice (cv. Kalojira). A = Absence of branch production, P = Presence of branch production.

Treatment	Main tiller (MT)				Secondary branch (SB)				Tertiary branch (TB)			
	Branch production	Leaf area (cm ²)		Longevity of MT (d)	Branch production	Leaf area (cm ²)		Longevity of (MT+SB) (d)	Branch production	Leaf area (cm ²)		Total longevity of (MT+SB+TB) (d)
		Flag	Second			Flag	Second			Flag	Second	
Control (Intact)	A	36	45	142	A	24	28	159	A	15	16	179
Removal of :												
25% Spikelets	A	36	45	142	A	24	28	159	A	15	16	179
50% Spikelets	P	36	45	142	A	24	28	159	A	15	16	179
75% Spikelets	P	36	45	146	P	24	28	163	A	15	16	182
100% Spikelets	P	36	45	149	P	24	28	166	A	15	16	186
Emasculated	P	36	45	149	P	24	28	166	A	15	16	186
Second leaf + 100% Spikelets	A	-	-	-	A	-	-	-	A	-	-	-

Table 40. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} , F.W.) in the flag, second and third leaf of main tiller of rice plant (cv. Rasi) during the progress of reproductive development.

Percentage removal of spikelets	Leaf Position	Days after anthesis					
		7		14		21	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
0 (Control)	Flag	1.18	78.4	0.73	64.8	0.31	51.8
	Second	0.95	65.9	0.62	60.3	0.34	49.4
	Third	0.74	60.3	0.54	54.5	0.17	42.2
25	Flag	1.10	81.6	0.75	64.3	0.32	50.6
	Second	0.94	66.7	0.65	61.8	0.33	47.8
	Third	0.71	58.9	0.51	52.3	0.18	40.8
50	Flag	1.08	76.1	0.76	65.1	0.36	54.8
	Second	0.96	71.5	0.61	62.3	0.34	48.3
	Third	0.69	59.5	0.53	55.1	0.16	43.1
75	Flag	1.01	76.9	0.83	66.6	0.39	55.1
	Second	0.96	68.7	0.64	62.5	0.36	53.3
	Third	0.73	61.2	0.55	54.2	0.18	42.5
100	Flag	1.11	80.1	0.80	68.1	0.47	60.2
	Second	0.92	72.3	0.62	58.4	0.37	55.5
	Third	0.70	60.5	0.56	53.3	0.18	44.1
Emasculated	Flag	1.03	80.2	0.81	67.0	0.41	62.8
	Second	0.98	74.9	0.65	60.6	0.36	56.1
	Third	0.68	57.9	0.55	56.1	0.175	43.8
LSD at P = 0.05		0.0043	0.27	0.0064	0.47	0.008	1.03
						0.009	1.07

Table 41. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} , F.W.) in the flag, second and third leaf of main tiller of rice plant (cv. Kalofira) during the progress of reproductive development.

Percentage removal of spikelets	Leaf position	Days after anthesis											
		7			14			21			28		
		Chl.	Prot.		Chl.	Prot.		Chl.	Prot.		Chl.	Prot.	
0 (Control)	Flag	1.10	83.5		0.82	69.0		0.54	58.0		0.29	48.0	
	Second	0.94	76.2		0.71	62.0		0.49	54.0		0.21	45.0	
	Third	0.75	62.2		0.51	56.0		0.24	48.0		0.08	39.0	
25	Flag	1.03	82.2		0.80	70.1		0.53	57.0		0.28	48.9	
	Second	0.91	75.5		0.70	62.3		0.51	55.0		0.22	44.2	
	Third	0.73	64.3		0.52	55.5		0.23	47.0		0.08	38.8	
50	Flag	1.02	78.5		0.83	70.3		0.56	60.0		0.32	51.3	
	Second	0.93	77.2		0.72	64.0		0.54	55.0		0.24	47.5	
	Third	0.71	60.3		0.50	57.1		0.23	49.5		0.09	39.9	
75	Flag	1.06	77.1		0.86	72.3		0.58	63.4		0.36	53.4	
	Second	0.92	74.1		0.74	66.8		0.54	56.6		0.26	47.4	
	Third	0.74	61.1		0.53	58.5		0.76	50.1		0.095	41.2	
100	Flag	1.07	79.2		0.85	75.1		0.61	64.5		0.41	57.1	
	Second	0.95	73.4		0.75	65.2		0.58	57.3		0.31	49.2	
	Third	0.75	60.4		0.54	58.0		0.28	52.2		0.10	44.5	
Emasculated	Flag	1.05	76.5		0.84	74.5		0.62	63.5		0.38	56.5	
	Second	0.92	71.5		0.75	64.6		0.57	58.4		0.33	50.5	
	Third	0.72	61.8		0.53	57.5		0.27	54.1		0.11	45.3	
LSD at P = 0.05		NS	0.46		0.006	0.42		0.0084	0.64		0.0072	0.74	

Table 42. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} , F.W.) in the flag, second and third leaf of main tiller of wheat plant (cv. Sonalika) during the progress of reproductive development.

Percentage removal of spikelets	Leaf position	Days after anthesis					
		7		14		21	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
0 (Control)	Flag	1.09	64.0	0.74	58.0	0.46	49.2
	Second	1.01	60.0	0.72	52.0	0.37	44.0
	Third	0.79	54.5	0.53	47.0	0.21	39.5
25	Flag	1.06	62.2	0.75	57.0	0.47	50.5
	Second	1.00	60.4	0.71	51.0	0.36	44.0
	Third	0.80	55.5	0.51	48.0	0.22	38.3
50	Flag	1.03	65.0	0.77	59.0	0.45	48.0
	Second	0.98	60.3	0.71	54.0	0.35	45.4
	Third	0.76	54.5	0.52	47.0	0.22	40.2
75	Flag	1.05	61.6	0.74	59.5	0.48	51.0
	Second	1.01	59.0	0.72	53.2	0.38	43.0
	Third	0.78	55.7	0.54	48.1	0.21	40.4
100	Flag	1.03	62.5	0.79	60.3	0.52	54.0
	Second	0.99	58.0	0.75	58.2	0.40	47.5
	Third	0.75	56.0	0.53	50.3	0.24	40.0
Emasculated	Flag	1.03	63.0	0.78	61.1	0.54	53.2
	Second	0.94	58.0	0.73	57.7	0.39	48.6
	Third	0.78	55.2	0.55	49.2	0.26	41.0
LSD at P = 0.05		NS	0.32	0.0051	0.44	0.003	0.45
						0.006	0.52

Table 43. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} . FW) in the flag and second leaf of secondary branch of rice plant (cv. Rasi) during the progress of reproductive development.

Percentage removal of spikelets	Leaf position	Days after anthesis							
		7		14		21		28	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
0 (Control)	Flag	0.99	72.2	0.71	62.9	0.29	50.2	0.11	38.2
	Second	0.91	70.2	0.66	58.5	0.28	48.3	0.16	42.6
25	Flag	0.93	73.2	0.68	63.6	0.306	52.1	0.11	38.5
	Second	0.94	71.1	0.65	58.8	0.29	47.7	0.175	43.7
50	Flag	0.98	75.8	0.69	60.4	0.34	52.4	0.13	42.0
	Second	0.91	69.3	0.69	59.9	0.33	50.3	0.165	44.5
75	Flag	0.92	75.3	0.72	66.3	0.37	56.0	0.16	48.3
	Second	0.92	69.3	0.66	60.1	0.34	52.2	0.162	44.65
100	Flag	0.92	76.3	0.72	67.3	0.394	60.2	0.192	51.9
	Second	0.93	64.1	0.67	58.5	0.34	55.3	0.185	47.8
Emasculated	Flag	0.96	76.1	0.75	67.3	0.39	59.2	0.19	50.7
	Second	0.93	66.6	0.65	60.3	0.35	58.8	0.16	48.5
LSD at P = 0.05		0.0063	0.87	0.005	0.42	0.0074	1.06	0.80	1.36

Table 44. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} , FW) in the flag and second leaf of secondary branch of rice plant (cv. Kalojira) during the progress of reproductive development.

Percentage removal of spikelets	Leaf position	Days after anthesis					
		7		14		21	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
0 (Control)	Flag	0.98	80.3	0.80	67.0	0.52	54.0
	Second	0.91	74.5	0.72	61.0	0.46	49.0
25	Flag	0.96	79.5	0.81	66.5	0.50	53.0
	Second	0.92	73.5	0.70	60.2	0.47	50.2
50	Flag	0.97	78.5	0.80	66.4	0.52	58.0
	Second	0.90	72.8	0.71	62.3	0.47	53.3
75	Flag	0.95	77.9	0.82	68.7	0.54	57.0
	Second	0.89	74.4	0.70	63.2	0.48	54.4
100	Flag	0.96	76.5	0.84	69.9	0.58	61.0
	Second	0.91	70.3	0.72	64.5	0.51	55.0
Emasculated	Flag	0.92	75.3	0.83	69.4	0.57	60.2
	Second	0.90	71.3	0.72	64.8	0.52	56.0
LSD at 0 = 0.05		NS	0.46	0.003	0.64	0.006	0.78
						0.008	0.84

Table 45. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} . FW) in the flag and second leaf of tertiary branch of rice plant (cv. Rasi) during the progress of reproductive development

Percentage removal of spikelets	Leaf position	Days after anthesis							
		7		14		21		28	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
0 (Control)	Flag	0.89	73.2	0.71	62.2	0.30	51.1	0.09	38.2
	Second	0.86	70.2	0.57	58.3	0.26	48.2	0.15	42.3
25	Flag	0.88	74.3	0.70	62.3	0.304	52.3	0.08	38.9
	Second	0.86	70.5	0.59	57.2	0.25	48.8	0.14	41.1
50	Flag	0.91	70.2	0.65	60.3	0.31	53.7	0.11	39.0
	Second	0.85	71.9	0.64	57.7	0.27	50.3	0.16	42.2
75	Flag	0.95	79.2	0.69	65.5	0.33	58.1	0.14	44.5
	Second	0.93	72.7	0.66	63.3	0.32	51.1	0.18	44.9
100	Flag	0.95	81.1	0.73	67.7	0.35	58.2	0.17	46.5
	Second	0.94	73.3	0.66	64.6	0.34	52.5	0.19	48.5
Emasculated	Flag	0.91	75.6	0.74	66.6	0.33	57.7	0.16	45.1
	Second	0.90	75.2	0.65	65.0	0.32	54.9	0.17	47.3
LSD at P = 0.05		0.0084	0.64	0.009	0.94	0.004	0.71	0.01	0.66

Table 46. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g^{-1} FW) in the flag and second leaf of tertiary branch of rice plant (cv. Kalojira) during the progress of reproductive development.

Percentage removal of spikelets	Leaf position	Days after anthesis							
		7		14		21		28	
		Chl.	Prot.	Chl.	Prot.	Chl.	Prot.	Chl.	Prot.
0 (Control)	Flag	0.96	74.0	0.79	63.0	0.50	50.0	0.18	40.0
	Second	0.90	72.0	0.68	58.0	0.47	47.0	0.14	35.0
25	Flag	0.95	71.0	0.78	64.0	0.49	51.0	0.18	41.0
	Second	0.91	70.0	0.65	58.0	0.46	46.0	0.15	35.7
50	Flag	0.97	70.5	0.79	62.0	0.51	51.0	0.19	40.2
	Second	0.92	70.0	0.67	59.0	0.47	47.0	0.15	36.7
75	Flag	0.95	71.2	0.78	65.0	0.54	56.0	0.21	42.0
	Second	0.89	70.3	0.69	59.0	0.51	51.0	0.19	40.0
100	Flag	0.98	72.0	0.79	66.0	0.55	58.0	0.26	46.5
	Second	0.90	69.0	0.70	62.0	0.52	52.0	0.22	42.0
Emasculated	Flag	0.94	71.5	0.78	65.0	0.56	57.0	0.28	48.4
	Second	0.90	69.2	0.70	60.0	0.52	53.0	0.23	43.6
LSD at P = 0.05		NS	0.34	0.004	0.38	0.006	0.72	0.007	0.84

Table 47. Effect of different treatments on whole plant senescence of two rice and one wheat cultivars.

Species	Cultivar	Treatment	Delay of senescence over control in days
Rice	Rasi	BA	7
		(BA + GA ₃)	10
		Panicle removed at the anthesis stage	10
		100% Spikelet removed from the main tiller	9
		Main tiller with secondary branch	28
	Kalojira	Main tiller with secondary and tertiary branch	44
		BA	7
		(BA + GA ₃)	11
		Panicle removed at the anthesis stage	12
		100% Spikelet removed from the main tiller	12
Wheat	Sonalika	Main tiller with secondary branch	24
		Main tiller with secondary and tertiary branch	42
		BA	7
		(BA + GA ₃)	10
		Panicle removed at the anthesis stage	6
		100% Spikelet removed	7
		(No secondary or tertiary branch developed)	

Table 48. Effect of normal and unfavourable photoperiod on flowering and senescence of four photoperiod sensitive rice cultivars.

Cultivar	Appearance of anthesis at the plant age under	
	Favourable photoperiod	Unfavourable photoperiod
Kalajira	115	304
Badsabhog	116	300
Patnai	120	312
Kalma	118	310

LITERATURE CITED

1. Abeles, F.B. 1973. Ethylene in Plant Biology. Academic Press, New York, pp.153-160.
2. Abraham, G. and L.Reinhold. 1980. Mechanism of effect of ageing on membrane transport in leaf strips of Centranthus ruber : Possible ethylene involvement in cutting shock. Planta. 150 : 380-384.
3. Abu-Shakra, S.S., Phillips, D.A. and R.C.Huffaker. 1978. Nitrogen fixation and delayed leaf senescence in soybeans. Science. 199 : 973-975.
4. Adedipe, N.O., Hunt, L.A. and R.A.Fletcher. 1971. Effects of benzyladenine on photosynthesis, growth and senescence of the bean plant. Physiol.Plant. 25 : 151-153.
5. Aharoni, N. and M.Lieberman. 1979. Ethylene as a regulator of senescence in tobacco (Nicotiana tabacum) leaf discs. Plant Physiol. 64 : 801-804.
6. Aharoni, N., Anderson, J.D. and M.Lieberman. 1979. Production and action of ethylene in senescing leaf discs : Effect of indole acetic acid, kinetin, silver ion and carbondioxide. Plant Physiol. 64 : 805-809.
7. Aharoni, N., Lieberman, M. and H.D.Sisler. 1979. Patterns of ethylene production in senescing leaves. Plant Physiol. 64 : 796-800.
8. Allison, J.C.S. and H.Weinmann. 1970. Effect of the absence of developing grain on carbohydrate content and senescence of maize leaves. Plant Physiol. 46 : 435-436.

9. Ambler, J.R., Morgan, P.W. and W.R. Jordan. 1983. Cytokinin concentrations in xylem sap of senescent and nonsenescent sorghum. *Plant Physiol.* 72 : 168-171.
10. Ambler, J.R., Morgan, P.W. and W.R. Jordan. 1987. Genetic Regulation of senescence in tropical grasses. In : *Plant Senescence : its Biochemistry and Physiology* (eds. W.W. Thomson, E.A. Nothnagel, and R.C. Huffaker), pp. 43-53. *Am. Soc. Plant Physiol.* Maryland.
11. Arnon, D.I. 1949. Copper enzymes in isolated chloroplasts : Polyphenoloxidases in Beta vulgaris. *Plant Physiol.* 24 : 1-15.
12. Aspinall, D. 1980. Role of abscisic acid and other hormones in adaptation to water stress. In : *Adaptation of plant to water and high temperature stress* (eds. N.C. Turner and P.J. Kramer) pp. 155-172, John Wiley and Sons, New York.
13. Aspinall, D., Singh, T.N. and L.G. Paleg. 1973. Stress metabolism. V. Absciscic acid and nitrogen metabolism in barley and Lolium temulentum L. *Aust. J. Biol. Sci.* 26 : 319-329.
14. Bangerth, F. 1989. Dominance among fruit/sinks and the search for a correlative signal. *Physiol. Plant.* 76 : 608-614.
15. Barber, R.F. and J.E. Thompson. 1983. Neutral lipids rigidify unsaturated acyl chains in senescing membranes. *J. Exp. Bot.* 34 : 268-276.
16. Barlow, P.W. 1982. Cell death. An integral part of plant development. In : *Growth Regulators in Plant Science* (eds. M.B. Jackson, B. Grant and I.A. Mackenzie), Monogr. 8. pp. 27-45. *British Plant Growth Regulator Group*, Wantage, England.
17. Barlow, P.W. and D.J. Carr (eds.). 1984. *Positional controls in Plant development*, Cambridge Univ. Press, London and New York.

18. Bata, J. and M. Neskovic. 1974. The effect of gibberellic acid and Kinetin on chlorophyll retention in Lemna trisulca L. Z.Pflanzen.Physiol. 73 : 84-88.
19. Bates, L.S., Waldren, R.P. and I.D. Teare. 1973. Rapid estimation of free proline for water stress studies. Plant Soil. 39 : 205-207.
20. Beever, J.E. and H.W. Woolhouse. 1973. Increased cytokinin from roots of Perilla frutescens during flower and fruit development. Nature (New Biol.). 246 : 149-150.
21. Beever, J.E. and H.W. Woolhouse. 1974. Inter-relationships of flowering, root growth and senescence in Perilla frutescens. In : Mechanisms of Regulation of Plant Growth Bulletin, 12 (eds. R.L. Bielecki, A.R. Ferguson and N.M. Cresswell), pp. 681-686. Roy. Soc. New Zealand, Wellington.
22. Beevers, L. 1976. Senescence. In : Plant Biochemistry (eds. J. Bonner and J.E. Varner), pp. 771-794. Academic Press, New York.
23. Below, F.E., Crafts-Brandner, S.J. and R.H. Hageman. 1985. Effect of foliar applications of urea on accelerated senescence of maize induced by ear removal. Plant Physiol. 79 : 1077-1079.
24. Benner, J.L. and L.D. Nooden. 1984. Translocation of photosynthate from soybean leaves to the pods during senescence. Biochem. Physiol. Pflanzen. 179 : 269-275.
25. Bernier, G., Kinet, J.M. and R.M. Sachs. 1981. The physiology of flowering. Vol. 2, CRC Press, Boca Raton, Florida.
26. Bewley, J.D. and M. Black. 1985. Seed Physiology of Development and Germination, Plenum, New York.
27. Bhatia, P.K. and Y.P. Abrol. 1987. Profiles of proteolytic activities during senescence of primary leaves of mung bean. (Vigna radiata L. Wilezek). Indian Acad. Sci. Plant Sci. 97 : 215-222.

28. Biswal,U.C., Choudhury,N.K. and B.Biswal. 1983. Degradation of plastid membranes during senescence. Indian Rev. Life Sci. 3 : 33-61.
29. Biswas,A.K. and M.A.Choudhuri. 1977. Analysis of yield components in relation to yield of rice sprayed with hormones and nutrients at different growth stages. Indian Agric. 21 : 33-39.
30. Biswas,A.K. and M.A.Choudhuri. 1978. Differential behaviour of the flag leaf of intact rice plant during ageing. Biochem.Physiol.Pflanzen. 173 : 220-228.
31. Biswas,A.K. and M.A.Choudhuri. 1978. Regulatory role of some hormones and nutrients on senescence development of soybean (Glycine max L.) leaf discs. Indian J.Exp.Biol. 6 : 1313-1314.
32. Biswas,A.K. and M.A.Choudhuri. 1980. Mechanism of monocarpic senescence in rice. Plant Physiol. 65 : 340-345.
33. Biswas,A.K. and M.A.Choudhuri. 1981. Influence of plant senescence as modified by hormones and nutrients on yield of rice. Indian Agric. 25 : 77-90.
34. Biswas,A.K. and A.K.Ghosh. 1989. Monocarpic senescence in relation to yield of Sesamum indicum during source-sink alteration. J.Agron.Grop Sci. 162 : 342-346.
35. Biswas,A.K. and S.K.Mondal. 1986. Monocarpic senescence in wheat : Influence of sterile glumes and ear. Physiol.Plant. 67 : 431-434.
36. Biswas,A.K. and S.K.Mondal. 1986. Regulation by kinetin and abscisic acid of correlative senescence in relation to grain maturation, source-sink relationship and yield of rice (Oryza sativa L.). Plant Growth Regulator. 4 : 239-245.
37. Biswas,A.K. and S.K.Mondal. 1987. Regulation of monocarpic senescence of Brassica campestris by developing pods. Physiol.Plant. 71 : 89-94.

38. Biswas, A.K. and S.K. Mondal. 1987. Whole plant senescence in Pennisetum typohoides : Implication of source-sink relationship. J. Plant Physiol. 127 : 371-377.
39. Biswas, A.K. and S.K. Mondal. 1988. Grain filling in relation to monocarpic senescence of wheat in varying source-sink ratios. Biol. Plant. 30 : 42-47.
40. Blum, A. 1985. Photosynthesis and transpiration in leaves and ears of wheat and barley varieties. J. Exp. Biol. 36 : 432-440.
41. Blum, A., Mayer, J. and G. Golan. 1988. The effect of grain number per ear (sink size) on source activity and its water relations in wheat. J. Exp. Bot. 39 : 106-114.
42. Bose, B. and H.S. Srivastava. 1979. Role of nitrate in delaying senescence of detached leaves. Indian J. Exp. Biol. 17 : 932-934.
43. Brady, C.J. 1988. Nucleic acid and protein synthesis. In : Senescence and Ageing in Plants (eds. L.D. Nooden and A.C. Leopold), pp. 147-179, Academic Press, New York.
44. Brinkman, M.A. and K.J. Frey. 1979. Flag leaf physiological analysis of oat isolines that differ in grain yield from their recurrent parents. Crop Science. 18: 69-73.
45. Brunetti, N., Rossi, L. and L. Ferrandi. 1975. Nitrate reductase and protease activity in ten varieties of durum wheat during the grain maturation stage. Genetica Agraria. 29 : 79-94.
46. Bui, M.B. and C.R. Stewart. 1983. Effect of NaCl on proline synthesis and utilization in excised barley leaves. Plant Physiol. 72 : 664-667.
47. Burke, J.J., Kalt-Torres, W., Swafford, J.R., Burton, J.W. and R.F. Wilson. 1984. Studies on genetic male-sterile soybeans. III. The initiation of monocarpic senescence. Plant Physiol. 75 : 1058-1063.

48. Burrows, W.J. and D.J. Carr. 1970. Cytokinin content of pea seeds during their growth and development. *Physiol. Plant.* 23 : 1064-1070.
49. Burton, K. 1956. A study of the conditions and mechanism of the diphenylamine reaction for the colorimetric estimation of deoxyribonucleic acid. *Biochem. J.* 62 : 315-323.
50. Butler, R.D. and E.W. Simon. 1971. Ultrastructural aspects of senescence in plants. *Adv. Gerontol. Res.* 3 : 73-129.
51. Callow, J.A. 1974. Ribosomal RNA, fraction-I protein synthesis, and ribulose diphosphate carboxylase activity in developing and senescing leaves of Cucumber. *New Phytol.* 73 : 13-20.
52. Callow, J.A., Callow, M.E. and H.W. Woolhouse. 1972. In vitro protein synthesis, ribosomal RNA synthesis and polyribosomes in senescing leaves of Perilla. *Cell Differentiation.* 1 : 79-90.
53. Camp, P.J., Huber, S.C. and D.E. Moreland. 1984. Changes in enzymes of sucrose metabolism and the activation of certain chloroplast enzymes during wheat leaf senescence. *J. Exp. Bot.* 35 : 659-668.
54. Chance, B. and A.C. Maehly. 1955. Assay of catalase and peroxidases. *Methods Enzymol.* 2 : 764-775.
55. Chang, D.Y., Miksche, J.P. and S.S. Dhillon. 1985. DNA changes involving repeated sequences in senescing soybean (Glycine max) cotyledon nuclei. *Physiol. Plant.* 64 : 409-417.
56. Chapin, F.S. and I.F. Wardlaw. 1988. Effect of phosphorus deficiency on source-sink interactions between the flag and developing grains in barley. *J. Exp. Bot.* 39 : 165-177.
57. Cherry, J.H. 1962. Nucleic acid determination in storage tissue of higher plants. *Plant Physiol.* 37 : 670-678.

58. Chia, L.S., Thompson, J.E. and E.B. Dumbroff. 1981. Stimulation of the effects of leaf senescence on membranes by treatment with paraquat. *Plant Physiol.* 67 : 415-420.
59. Chibnall, A.C. 1939. Protein metabolism in the plants. Yale Univ. Press, New Haven, Connecticut.
60. Chin, T. and L. Beevers. 1970. Changes in endogenous growth regulators in Nasturtium leaves during senescence. *Planta.* 92 : 178-188.
61. Choudhuri, M.A. 1988. Free radicals and leaf senescence A review. *Pl. Physiol. and Biochem.* 15 : 18-29.
62. Choudhuri, M.A. and S.K. Chatterjee. 1970. Seasonal changes in the levels of some cellular components in the abscission zone of Coleus leaves of different ages. *Ann. Bot.* 34 : 275-278.
63. Choudhuri, M.A. and K.K. Gupta. 1976. Transpiration. The loss of water from plants. In : *Practical Plant Physiology*, pp. 48-70. New Central Book Agency, Calcutta.
64. Choudhuri, M.A. and W.A. Mondal. 1988. Mechanism of monocarpic senescence in rice. *Indian Rev. Life Sci.* 8 : 3-28.
65. Christensen, L.E., Below, F.E. and R.H. Hageman. 1981. The effects of ear removal on senescence and metabolism of maize. *Plant Physiol.* 68 : 1180-1185.
66. Ciha, A.J., Brenner, M.L. and W.A. Burn. 1978. Effect of pod removal on abscisic acid levels in soybean tissue. *Crop. Sci.* 18 : 776-779.
67. Clarke, G.M. 1969. *Statistics and Experimental Design*. 1st edn. (ed. E. Arnold), pp. 91-100, Edward Arnold Ltd. London.
68. Colbert, K.A. and J.E. Beever. 1981. Effect of disbudding on root cytokinin export and leaf senescence in tomato and tobacco. *J. Exp. Bot.* 32 : 121-127.
69. Cole, R.D. 1984. A minireview of microheterogeneity in H1 histone and its possible significance. *Ann. Biochem.* 136 : 24-30.

70. Colquhoun, A.J. and J.R. Hillman. 1975. Endogenous abscisic acid and the senescence of leaves of Phaseolus vulgaris L. Z.Pflanzen.Physiol. 76 : 326-332.
71. Conrad, K. 1962. Über geschlechtsgebundene Unterschiede im wuchsstoffgehalt männlicher und weiblicher Hanfpflanzen, Flora. 152 : 68-73.
72. Crafts-Brandner, S.J. and D.B. Egli. 1987. Sink removal and leaf senescence in soybean. cultivar effects. Plant Physiol. 85 : 662-666.
73. Crafts-Brandner, S.J. and D.B. Egli. 1987. Modification of seed growth in soybean by physical restraint : Effect on leaf senescence. J.Exp.Bot. 38 : 2043-2049.
74. Crafts-Brandner, S.J., Below, F.E., Harper, J.E. and R.H. Hageman. 1984. Differential senescence of maize hybrids following ear removal. 1. Whole Plant. Plant Physiol. 74 : 360-367.
75. Crafts-Brandner, S.J., Below, F.E., Harper, J.E. and R.H. Hageman. 1984. Effects of pod removal on metabolism and senescence of nodulating and non-nodulating soybean isolate 1. Metabolic constituents. Plant Physiol. 75 : 311-317.
76. Crane, J.C. 1964. Growth substances in fruit setting and development. Annu.Rev.Plant Physiol. 15 : 303-326.
77. Crocker, W. 1939. Ageing in plants. In : Problems of Ageing (ed. E.V. Cowdry), 1st ed., pp.1-31, Williams & Wilkins, Baltimore, Maryland.
78. Croes, A.F., Hespen, P.L.G.M., Van De Loo, A.A.J. and G.W.M. Barendse. 1986. Protein synthesis during in vitro flower bud formation in tobacco. Acta Bot.Neerl. 35 : 161-167.
79. Cuello, J. and B. Sabater. 1982. Control of some enzymes of nitrogen metabolism during senescence of detached barley (Hordeum vulgare L.) leaves. Plant Cell Physiol. 23 : 561-565.

80. Cuello, J., Quiles, M.J. and B. Sabater. 1984. Role of protein synthesis and light in the regulation of senescence in detached barley leaves. *Physiol. Plant.* 60:133-138.
81. Curth, P. 1959. Vegetative zukerruben im sechsten vegetationsjahr. *Zuchter.* 29 : 374-375.
82. Curtis, O.F. and D.G. Clark. 1950. An introduction to plant Physiology, McGraw Hill, New York.
83. Dalling, M.J., Tang, A.B. and R.C. Huffaker. 1983. Evidence for the existence of peptide hydrolase activity associated with chloroplasts from barley mesophyll protoplasts. *Z. Pflanzen Physiol.* 111 : 311-318.
84. Davey, J.E. and J. Van Staden. 1978. Cytokinin activity in Lupinus albus. II. Distribution in fruiting plants. *Physiol. Plant.* 43 : 87-93.
85. Davey, J.E. and J. Van Staden. 1979. Cytokinin activity in Lupinus albus. IV. Distribution in seeds. *Plant Physiol.* 63 : 873-877.
86. Davies, P.J., Proebsting, W.M. and T.J. Gianfagna. 1977. Hormonal relationships in whole plant senescence. In : Plant Growth Regulation, 9th International Conference on Plant Growth Substances (ed. P.E. Pilet), pp. 273-280, Springer-Verlag, Berlin.
87. Debata, A. and K.S. Murty. 1981. Effect of growth regulating substances on leaf senescence in rice. Oryza. 18 : 177-179.
88. Deleo, P. and J.A. Sacher. 1970. Control of ribonuclease and acid phosphatase by auxin and abscisic acid during senescence of Rhoeo leaf sections. *Plant Physiol.* 46 : 806-811.
89. Derman, B.D., Rupp, D.C. and L.D. Nooden. 1978. Mineral distribution in relation to fruit development and monocarpic senescence in Anoka Soybeans. *Am. J. Bot.* 65 : 205-213.

90. Dingzi, L., Yuca, P., Yuefang, M., Zongda, L., Weiqun, B., Yiming, J. and Y. Shupeng. 1988. Physiological and biochemical studies on leaf senescence at heading and grain formation stage in hybrid rice. *Sci. Agric. Sin.* 21 : 21-26.
91. Dong, C.N. and R.N. Arteca. 1982. Changes in photosynthetic rates and growth following root treatments of tomato plants with phytohormones. *Photosynth. Res.* 3:45-52.
92. Dure, L., Galav, G., Chlan, C. and J. Pyle. 1983. Developmentally regulated gene sets in cotton embryogenesis. In : *Plant Molecular Biology* (ed. R.B. Goldberg), UCLA Symp. Mol. Cell. Biol. N.S. Vol. 12, pp. 331-342. Alan. R. Liss., New York.
93. Dwivedi, S., Kar, M. and D. Mishra. 1979. Biochemical changes in excised leaves of Oryza sativa subjected to water stress. *Physiol. Plant.* 45 : 35-40.
94. Dyer, T.A. and D.J. Osborne. 1971. Leaf nucleic acids. II. Metabolism during senescence and the effect of kinetin. *J. Exp. Bot.* 22 : 552-560.
95. El-Antably, H.M.M., Wareing, P.F. and J. Hillman. 1967. Some physiological responses to D-L abscisin (dormin). *Planta.* 73 : 74-90.
96. Elstner, E.F. 1982. Oxygen activation and oxygen toxicity. *Annu. Rev. Plant. Physiol.* 33 : 73-76.
97. Engvild, K.C. 1989. The death hormone hypothesis. *Physiol. Plant.* 77 : 282-285.
98. Evans, G.C. 1972. The quantitative analysis of plant growth. Blackwell, Oxford.
99. Evans, J.R. 1983. Nitrogen and photosynthesis in the flag leaf of wheat. (Triticum aestivum L.). *Plant Physiol.* 72 : 297-302.

100. Evans, L.T. and H.M. Rawson. 1970. Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. *Aust. J. Biological Science*. 23 : 245-254.
101. Even-Chen, Z. and C. Itai. 1975. The role of abscisic acid in senescence of detached tobacco leaves. *Physiol. Plant*. 34 : 97-100.
102. Feller, U.K., Soong, T.T. and R.H. Sageman. 1977. Leaf proteolytic activities and senescence during grain development of field grown corn (Zea mays L). *Plant Physiol*. 59 : 290-294.
103. Fick, N.G. and C.O. Qualset. 1975. Genetic control of endosperm amylase activity and gibberellin responses in standard-height and short-statured wheat. *Proc. Natl. Acad. Sci. USA*. 72 : 892-895.
104. Fischer, E., Raschke, K. and M. Stitt. 1986. Effects of abscisic acid on photosynthesis in whole leaves. Changes of CO₂ assimilation, levels of carbon-reduction cycle intermediates, and activity of ribulose-1,5-bisphosphate carboxylase. *Planta*. 164 : 536-545.
105. Fisher, R.A. and F. Yates. 1947. Statistical tables for biological agricultural and medical research. 6th edn., Longman.
106. Fletcher, R.A. and D. McCullagh. 1971. Cytokinin induced chlorophyll formation in cucumber cotyledons. *Planta*. 101 : 88-90.
107. Fletcher, R.A., Oegema, T. and R.F. Horton. 1969. Endogenous gibberellin levels and senescence in Taraxacum officinale. *Planta*. 86 : 98-102.
108. Foster, R.B. 1977. Tachigalia versicolor is a suicidal tree. *Nature*. 268 : 624-626.

109. Franceschi, V.R. and R.T. Giaquinta. 1983. The paraveinal mesophyll of soybean leaves in relation to assimilate transfer and compartmentation. II. Structural, metabolic and compartmental changes during reproductive growth. *Planta*. 157 : 422-431.
110. Fraser, D.E. and R.G.S. Bidwell. 1974. Photosynthesis and photorespiration during the ontogeny of the bean plant. *Can. J. Bot.* 52 : 2561-2570.
111. Fredeen, A.L., Rao, I.M. and N. Terry. 1989. Influence of phosphorus nutrition on growth and carbon partitioning in Glycine max. *Plant Physiol.* 89 : 225-230.
112. Friedrich, J.W. and R.C. Huffaker. 1980. Photosynthesis, leaf resistance and ribulose-1,5-bisphosphate carboxylase degradation in senescing barley leaves. *Plant. Physiol.* 65 : 1103-1107.
113. Galston, A.W. 1947. The effect of 2,3,5-tri-iodobenzoic acid on the growth and flowering of soybeans. *Am. J. Bot.* 34 : 356-360.
114. Garcia, S., Martin, M. and B. Sabater. 1983. Protein synthesis by chloroplasts during the senescence of barley leaves. *Physiol. Plant.* 57 : 260-266.
115. Garrison, F.R., Brinker, A.M. and L.D. Nooden. 1984. Relative activities of xylem supplied cytokinins in retarding soybean leaf senescence and sustaining pod development. *Plant. Cell Physiol.* 25 : 213-224.
116. Geiger, D.R. 1979. Control of partitioning and export of carbon in leaves of higher plants. *Bot. Gaz.* 140:241-248.
117. Gepstein, S. 1988. Photosynthesis. In : *Senescence and Ageing in Plants* (eds. L.D. Nooden and A.C. Leopold), pp.85-109. Academic Press, New York.
118. Gepstein, S. and K.V. Thimann. 1980. Changes in the abscisic acid content of oat leaves during senescence. *Proc. Natl. Acad. Sci. USA.* 77 : 2050-2053.

119. Gepstein, S. and K.V.Thimann. 1981. The role of ethylene in the senescence of oat leaves. *Plant Physiol.* 68 : 349-354.
120. Ghosh, A.K. and A.K.Biswas. 1989. Monocarpic senescence in Arachis hypogaea : Nutrient withdrawal vs. migration of senescence signal. *Indian J.Plant Physiol.* 32 : 172-174.
121. Gianfagna, T.J. and P.J.Davies. 1978. Fruit-induced apical senescence in a genetic line of peas. *Plant Physiol.* (Suppl), 61 : 26.
122. Gianfagna, T.J. and P.J.Davies. 1981. The relationship between fruit growth and apical senescence in the G-2 line of peas. *Planta.* 152 : 356-364.
123. Gianfagna, T.J. and P.J.Davies. 1983. The transport of substances out of developing fruits in relation to the induction of apical senescence in Pisum sativum line G-2. *Physiol.Plant.* 59 : 676-684.
124. Giannopolitis, C.N. and S.K.Ries. 1977. Superoxide dismutases. I. Occurrence in higher plants. *Plant Physiol.* 59 : 309-314.
125. Goldthwaite, J.J. and W.M.Laetsch. 1967. Regulation of senescence in bean leaf discs by light and chemical growth regulators. *Plant Physiol.* 42 : 1757-1762.
126. Gonthier, R., Jacquard, A. and G.Bernier. 1987. Changes in cell cycle duration and growth fraction in the shoot meristem of *Sinapis* during floral transition. *Planta.* 170:55-59.
127. Goodwin, P.B., Gollnow, B.I. and D.S.Letham. 1978. Phytohormones and growth correlations. In : *Phytohormones and Related compounds. A Comprehensive Treatise* (eds. D.S.Letham, P.B.Goodwin and T.J.V.Higgins), Vol.2, pp.215-249, Elsevier/North Holland, Amsterdam.
128. Gori, D.F. 1983. Post-pollination and adaptive floral changes. In : *Handbook of Experimental Pollination Biology* (eds. C.E.Jones and R.J.Little), pp.31-45. Van Nostrand-Reinhold, New York.

129. Gornall, A.C., Bardawill, C.J. and M.M. David. 1949. Determination of serum proteins by means of the biuret reaction. *J. Biol. Chem.* 177 : 751-766.
130. Goyal, V. and A. Pillai. 1986. Histochemical and cytophotometric estimation of DNA, RNA and protein in the shoot apex of Nicotiana tabacum Linn. *Cytologia*. 51:637-644.
131. Goyal, S.C., Jain, S. and A. Pillai. 1983. Localization and semiquantitative estimation of DNA, RNA and proteins in the shoot apex of Papaver somniferum. *Beitr. Biol. Pflanz.* 58 : 67-76.
132. Grabau, L.J., Blevins, D.G. and H.C. Minor. 1986. P-nutrition during seed development. Leaf senescence, pod retention and seed weight of soybean. *Plant Physiol.* 82 : 1008-1012.
133. Greening, M.T., Butterfield, F.J. and N. Harris. 1982. Chloroplast ultrastructure during senescence and regreening of flax cotyledons. *New Phytol.* 92 : 279-285.
134. Grossmann, K. and J. Jung. 1982. Pflanzlicher - seneszenzvorgänge *Z. Acker Pflanzenbau*. 151 : 149-165.
135. Grover, A., Koundal, K.R. and S.K. Sinha. 1985. Senescence of attached leaves : Regulation by developing pods. *Physiol. Plant.* 63 : 87-92.
136. Guera, A., Martin, M. and B. Sabater. 1989. Subchloroplast localization of polypeptides synthesized by chloroplasts during senescence. *Physiol. Plant.* 75 : 382-388.
137. Hall, A.J. and C.J. Brady. 1977. Assimilate source-sink relationships in Capsicum annum L. II. Effects of fruiting and defloration on the photosynthetic capacity and senescence of the leaves. *Aust. J. Plant. Physiol.* 4 : 771-783.
138. Hall, N.P., Keys, A.J. and M.J. Merrett. 1978. Ribulose-1,5-diphosphate carboxylase protein during flag leaf senescence. *J. Exp. Bot.* 29 : 31-37.

139. Hamilton,D.A. and P.J.Davies. 1988. Sucrose and malic acid as the compounds exported to the apical bud of pea following $^{14}\text{CO}_2$ labelling of the fruit. No evidence for a senescence factor. Plant Physiol. 86 : 465-472.
140. Hamilton,D.A. and P.J.Davies. 1988. Export of organic materials from developing fruits of pea and its possible relation to apical senescence. Plant Physiol. 86 : 951-955.
141. Hamilton,D.A. and P.J.Davies. 1988. Mechanism of export of organic material from the developing fruit of pea. Plant Physiol. 86 : 956-959.
142. Hardwick,K., Wood,M. and H.W.Woolhouse. 1968. Photosynthesis and respiration in relation to leaf age in Perilla frutescens L. Brit.New Phytol. 67 : 79-86.
143. Harris,G.C., Cheeseborough,J.K. and D.A.Walker. 1983. Measurement of CO_2 and H_2O vapor exchange in spinach leaf discs. Effect of orthophosphate. Plant Physiol. 71 : 102-107.
144. Harris,J.B. and H.Arnett. 1973. Effects of senescence on chloroplasts of the tobacco leaf. Tissue and Cell. 5 : 527-544.
145. Harris,J.B., Schaefer,V.G., Dhillon,S.S. and J.P.Miksche. 1982. Differential decline in DNA of ageing leaf tissue. Plant Cell Physiol. 23 : 1267-1273.
146. Hartung,W. 1977. Der Transport Von (2- ^{14}C) abscisinsäure aus der Wurzelsystem intakte Bohnen-keimlinge in die oberirdischen Teile der Pflanze. Z.Pflanzenphysiol. 83 : 81-84.
147. Head,G.C. 1973. Shedding of roots. In : Shedding of plant parts. (ed. T.T.Kozlowski), pp.237-293, Academic Press, New York.

148. Heath, R.L. and L. Packer. 1968. Photoperoxidation in isolated chloroplasts. I. Kinetics and stoichiometry of fatty acid peroxidation. Arch. Biochem. Biophys. 125:189-198.
149. Heaton, T., Lee, A. and G. Tallman. 1987. Stomata in senescing leaves : guard cell viability and regulation of stomatal function in Nicotiana glauca. In : Plant Senescence : Its Biochemistry and Physiology (eds. W.W. Thomson, E.A. Nothnagel and R.C. Huffaker), pp.198-214. Am. Soc. Plant. Physiol., Maryland.
150. Heindl, J.C., Carlson, D.R., Burn, W.A. and M.L. Brenner. 1982. Ontogenetic variation of four cytokinins in soybean root pressure exudate. Plant Physiol. 70:1619-1625.
151. Herzog, H. 1982. Relation of source and sink during grain-filling period in wheat and some aspects of its regulation. Physiol. Plant. 56 : 155-160.
152. Hicks, D.R. 1978. Growth and Development. In : Soybean Physiology, Agronomy and Utilization (ed. A.G. Norman), pp.27-44, Academic Press, New York.
153. Hildebrand, F. 1982. Die Lebensdauer und vegetationsweise der pflanzen, ihre Ursachen und ihre Entwicklung. Bot. Jahrb. 2 : 51-135.
154. Hillman, J.R., Yeang, H.C. and V.J. Fairhurst. 1985. Ethylene, lateral bud growth and indole-3-acetic acid transport. In : Ethylene and Plant Development (eds. J.A. Roberts and G.A. Tucker), pp.213-217, Butterworths, London.
155. Hodge, E.T. and J.A. Sacher. 1975. Effects of kinetin, auxin and abscisic acid on ribonuclease and acid phosphatase during senescence of leaf tissue. Biochem. Physiol. Pflanzen. 168 : 433-441.
156. Housley, S. and N.M. Griffiths. 1962. Cited by Mishra, D. and B. Mishra 1973 in Retardation of induced senescence of leaves from crop plants by benzimidazole and cytokinin. Exp. Geront. 8 : 235-239.

157. Hsia, C.P. and C.H.Kao. 1978. The importance of roots in regulating senescence of soybean primary leaves. *Physiol.Plant.* 43 : 385-389.
158. Huff, A. and C.D.Dybing. 1980. Factors affecting shedding of flowers in soybean (Glycine max L. Merrill). *J.Exp.Bot.* 31 : 751-762.
159. Hurng, W.P., Lin, T.L., Ren, S.S., Chen, J.C., Chen, Y.R. and C.H.Kao. 1988. Senescence of rice leaves. XVIII. Changes of stomatal aperture during senescence. *Plant Cell Physiol.* 29 : 27-31.
160. Incoll, L.D. and P.C.Jewer. 1987. Cytokinins and stomata. In : *Stomatal Function* (eds. E.Zeiger, G.D.Farquhar and I.R.Cowan), pp.281-292, Stanford Univ, Press, Stanford, California.
161. Israel, D.W., Burton, J.W. and R.F.Wilson. 1985. Studies on genetic male sterile soybeans. IV. Effect on male sterility and source of nitrogen nutrition on accumulation, partitioning and transport of nitrogen. *Plant Physiol.* 78 : 762-767.
162. Itai, C. and Y.Vaadia. 1971. Cytokinin activity in water stressed shoots. *Plant Physiol.* 47 : 87-90.
163. Itai, C., Richmond, A. and Y.Vaadia. 1968. The role of root cytokinins during water and salinity stress. *Isr.J.Bot.* 17 : 187-195.
164. Jacquard, A. and C.Houssa. 1988. DNA fiber replication during a morphogenetic switch in the shoot meristematic cells of higher plant. *Experimental cell Research.* 179 : 454-461.
165. Jacquard, A., Miksche, J.P. and G.Bernier. 1972. Quantitative study of nucleic acids and proteins in the shoot apex of Sinapis alba during transition from the vegetative to the reproductive condition. *Am.J.Bot.* 59 : 714-721.

166. Jaffe, M.J. and A.W. Galston. 1966. Physiological studies on pea seedlings. II : The role of light and ATP in contact coiling. *Plant Physiol.* 41 : 1152-1158.
167. James, A.L., Anderson, I.C. and H.A.L. Greer. 1965. Effects of naphthalene acetic acid on field grown soybeans. *Crop.Sci.* 5 : 472-474.
168. Janick, J. and A.C. Leopold. 1961. A distinction between bolting and flowering effects on senescence. *Nature.* 192 : 887-888.
169. Janzen, D.H. 1976. Why bamboos wait so long to flower. *Annu.Rev.Ecol.Syst.* 7 : 347-391.
170. Jenkins, G.I. and H.W. Woolhouse. 1981 . Photosynthetic electron transport during senescence of the primary leaves of Phaseolus vulgaris L. II. The activity of photosystem one and two, and a note on the site of reduction of ferricyanide. *J.Exp.Bot.* 32 : 989-997.
171. Jewer, P.C. and L.D. Incoll. 1980. Promotion of stomatal opening in the grass Antheophora pubescens Nees by a range of natural and synthetic cytokinins. *Planta.* 150 : 218-221.
172. Kao, C.H. 1977. Senescence of rice leaves. I. Comparison between detached and intact leaves. *Mem.Coll.Agric. Natl.Taiwan Univ.* 17 : 12-18.
173. Kao, C.H. 1978. Senescence of rice leaves. II. Antisenescent action of cytokinins. *Proc.Natl.Sci.Counc.* 2 : 391-398.
174. Kao, C.H. 1979. Senescence of rice leaves. III. The inter-organ control of leaf senescence of rice seedlings. *Proc.Natl.Sci.Counc. ROC.* 3 : 199-204.
175. Kao, C.H. 1980. Retardation of senescence by low temperature and benzyladenine in intact primary leaves of soybean. *Plant Cell Physiol.* 21 : 339-344.

176. Kao, C.H. and S.F. Yang. 1983. Role of ethylene in the senescence of detached rice leaves. *Plant Physiol.* 73 : 881-885.
177. Kar, M. and J. Feierabend. 1984. Metabolism of activated oxygen in detached wheat and rye leaves and its relevance to the initiation of senescence. *Planta.* 160 : 385-391.
178. Kar, M. and J. Feierabend. 1984. Changes in the activities of enzymes involved in amino acid metabolism during the senescence of detached wheat leaves. *Physiol. Plant.* 62 : 39-44.
179. Kar, M. and D. Mishra. 1976. Catalase, peroxidase and polyphenol oxidase activities during rice leaf senescence. *Plant Physiol.* 57 : 315-319.
180. Karp, G. 1984. *Cell Biology.* McGraw Hill, New York, pp. 600.
181. Kelly, M.O. and P.J. Davies. 1986. Genetic and photoperiodic control of the relative rates of reproductive and vegetative development in peas. *Ann. Bot.* 58 : 13-21.
182. Kelly, M.O. and P.J. Davies. 1988. Photoperiodic and genetic control of carbon partitioning in peas and its relationship to apical senescence. *Plant Physiol.* 86 : 978-982.
183. Kelly, M.O. and P.J. Davies. 1988. The control of whole plant senescence. *CRC Crit. Rev. Plant Sci.* 7 : 139-173.
184. Kende, H. 1971. The cytokinins. *Int. Rev. Cytol.* 31 : 301-338.
185. Khanna-Chopra, R. and S.K. Sinha. 1981. RUBP carboxylase activity in wheat following ear emergence and evaluation of the role of ear. *Photosynth. Res.* 2 : 145-152.
186. Kim, Y.J., Hwang, I., Tres, L.L., Kierszenbaum, A.L. and C.B. Chae. 1987. Molecular cloning and differential expression of somatic and testis-specific H2B histone genes during rat spermatogenesis. *Dev. Biol.* 124:23-24.

187. Kishitani, S. and S. Tsunoda. 1985. Differences in the photosynthetic response to air humidity among rice varieties with special reference to xylem-vessel size. Japanese J. Breed. 35 : 268-274.
188. Koller, H.R. and J.H. Thorne. 1978. Soybean pod removal alters leaf diffusion resistance and leaflet orientation. Crop. Sci. 18 : 305-307.
189. Kriedeman, P.E., Loveys, B.R., Fuller, G.L. and A.C. Leopold. 1972. Abscissic acid and stomatal regulation. Plant Physiol. 49 : 743-750.
190. Krizek, D.T., McIlrath, W.J. and B.S. Vergara. 1966. Photoperiodic induction of senescence in Xanthium plants. Science. 151 : 95-96.
191. Kruh, J., Defer, N., Kitzis, A., Leibovitch, M.P. and L. Tichonicky. 1979. Chromatin proteins and genetic control. C.R. Seances Soc. Bio. Fil. 173 : 331-334.
192. Kulaeva, O.N. 1962. The effect of roots on leaf metabolism in relation to the action of kinetin on leaves. Soviet. Plant Physiol. 9 : 182-189.
193. Kulkarni, V.J. and W.W. Schwabe. 1985. Graft transmission of long day-induced leaf senescence in Kleinia articulata, J. Exp. Bot. 36 : 1620-1633.
194. Kumar, K.B. and P.A. Khan. 1983. Induction and suppression of RNase activity by growth regulators in senescing ragi leaves. Physiol. Plant. 58 : 479-485.
195. Kumar, S. and K.K. Nanda. 1981. Gibberellic acid and salicylic acid causes changes in RNA associated with floral induction in Impatiens balsamina exposed to inductive and non-inductive photoperiod. Indian J. Exp. Biol. 19 : 961-965.
196. Kunert, K.J. 1984. The diphenyl-ether herbicide oxyfluorfen : A potent inducer of lipid peroxidation in higher plants. Z. Naturforsch. 39C : 476-481.

197. Lamattina, L., Lezica, R.P. and R.D. Conde. 1985. Protein metabolism in senescing wheat leaves. Determination of synthesis and degradation rates and their effects on protein loss. *Plant Physiol.* 77 : 587-590.
198. Lamattina, L., Anchoverri, V., Conde, R.D. and R.P. Lezica. 1987. Quantification of the kinetin effect on protein synthesis and degradation in senescing wheat leaves. *Plant Physiol.* 83 : 497-499.
199. Lampa, G.K., Elliot, L.V. and A.J. Bendica. 1980. Changes in chloroplast number during pea leaf development. An analysis of protoplast population. *Planta.* 148:437-443.
200. La Rue, T.A. and W.G.W. Kurz. 1973. Estimation of nitrogenase using a colorimetric determination for ethylene. *Plant Physiol.* 51 : 1074-1075.
201. Lau, O.L. and S.F. Yang. 1976. Synergistic effect of calcium and kinetin on ethylene production of mung bean hypocotyl. *Planta.* 118 : 1-16.
202. Lawrie, A.C. and C.T. Wheeler. 1974. The effects of flowering and fruit formation on the supply of photosynthetic assimilates to the nodules of P. sativum L. in relation to the fixation of nitrogen. *New Phytol.* 73 : 1119-1127.
203. Lawton, K.A., Raghothama, K.G., Goldsbrough, P.B. and W.R. Woodson. 1990. Regulation of senescence-related gene expression in carnation flower petals by ethylene. *Plant Physiol.* 93 : 1370-1375.
204. Lehninger, A.L. 1975. In : *Biochemistry*. Kalyani Pubs., New Delhi, p.997.
205. Lenz, F. and C.N. Williams. 1973. Effect of fruit removal on net assimilation and gaseous diffusive resistance of soybean leaves. *Angew. Bot.* 47 : 59-63.
206. Leopold, A.C. 1961. Senescence in plant development. The death of plants or plant parts may be of positive ecological or physiological value. *Science.* 134:1727-1732.

207. Leopold, A.C. 1975. Ageing, senescence and turnover in plants. *Bioscience*. 25 : 659-662.
208. Leopold, A.C. 1980. Ageing and senescence in plant development. In : *Senescence in Plants* (ed. K.V.Thimann), pp.1-12, CRC Press, Boca Raton, Florida.
209. Leopold, A.C. and L.D.Nooden. 1984. Hormonal regulatory systems in plants. *Encycl.Plant Physiol. New.Ser.* 10 : 4-22.
210. Leopold, A.C., Niedergang-Kamien, E. and J.Janick. 1959. Experimental modification of plant senescence. *Plant Physiol.* 34 : 570-573.
211. Letham, D.S. 1978. Cytokinins. In : *Phytohormones and Related Compounds - A Comprehensive Treatise, Vol.1* (eds. D.S.Letham, P.B.Goodwin, and T.J.V.Higgins), pp.205-263, Elsevier/North Holland, Amsterdam.
212. Lindoo, S.J. and L.D.Nooden. 1976. The interrelation of fruit development and leaf senescence in 'Anoka' soybeans. *Bot.Gaz.* 137 : 218-223.
213. Lindoo, S.J. and L.D.Nooden. 1977. Studies on the behaviour of the senescence signal in Anoka soybeans. *Plant Physiol.* 59 : 1136-1140.
214. Lindoo, S.J. and L.D.Nooden. 1978. Correlation of cytokinins and abscisic acid with monocarpic senescence in soybeans. *Plant Cell Physiol.* 19 : 997-1006.
215. Loveys, B.R. and P.E.Kriedemann.. 1974. Internal control of stomatal physiology and photosynthesis. I. Stomatal regulation and associated changes in endogenous levels of abscisic and phaseic acids. *Aust.J.Plant Physiol.* 1 : 407-415.
216. Lowry, O.H., Rosebrough, N.J., Farr, A.L. and R.J.Randall. 1951. Protein measurement with Folin-Phenol reagent. *J.Biol.Chem.* 193 : 265-275.

217. Lyndon, R.F., Jacqumard, A. and G. Bernier. 1983. Changes in protein composition of the shoot meristem during floral evocation in Sinapsis alba. *Physiol. Plant.* 59 : 476-480.
218. MacKown, C.T., Van Sanford, D.A. and Y.Z. Ma. 1989. Main stem sink manipulation in wheat. Effect on nitrogen allocation to tillers. *Plant Physiol.* 89 : 597-601.
219. Mae, T. and K. Ohira. 1984. The relationship between proteolytic activity and loss of soluble protein in rice (Oryza sativa L.) leaves from anthesis through senescence. *Soil. Sci. Plant Nutr.* 30 : 427-434.
220. Mae, T., Makino, A. and K. Ohira. 1983. Changes in the amounts of ribulose biphosphate carboxylase synthesized and degraded during the life span of rice leaf (Oryza sativa L.). *Plant Cell Physiol.* 24 : 1079-1086.
221. Mae, T., Makino, A. and K. Ohira. 1987. Carbon fixation and changes with senescence in rice leaves. In : *Plant Senescence : Its Biochemistry and Physiology* (eds. W.W. Thomson, E.A. Nothnagel and R.C. Huffaker), pp. 123-131, Am. Soc. Plant Physiol., Maryland.
222. Makino, A., Mae, T. and K. Ohira. 1983. Photosynthesis and ribulose, 1,5-bisphosphate carboxylase in rice leaves. Changes in photosynthesis and enzyme involved in carbon assimilation from leaf development through senescence. *Plant Physiol.* 73 : 1002-1007.
223. Makino, A., Mae, T. and K. Ohira. 1984. Relation between nitrogen and ribulose 1,5-bisphosphate carboxylase in rice leaves from emergence through senescence. *Plant Cell Physiol.* 25 : 429-437.
224. Makino, A., Mae, T. and K. Ohira. 1985. Photosynthesis and ribulose 1,5-bisphosphate carboxylase/oxygenase in rice leaves from emergence through senescence. Quantitative analysis by carboxylation/oxygenation and regeneration of ribulose 1,5-bisphosphate. *Planta.* 166 : 414-420.

225. Makrides, S.C. and J. Goldthwaite. 1981. Biochemical changes during bean leaf growth, maturity and senescence content of DNA, polyribosomes, ribosomal RNA, protein and chlorophyll, J. Exp. Bot. 32 : 725-735.
226. Malik, N.S.A. 1987. Senescence in oat leaves. Changes in translatable m-RNA. Physiol. Plant. 70 : 438-446.
227. Malik, N.S.A. and A.M.M. Barrie. 1975. Correlative effects of fruits and leaves in senescence of pea plants. Planta. 124 : 169-175.
228. Malik, N.S.A. and A.M.M. Barrie. 1977. Changes in leaf proteins of pea, Pisum sativum L. during development on defoliated plants. Plant Physiol. 59 : 331-334.
229. Malik, N.S.A. and A.M.M. Barrie. 1980. The role of root in shoot senescence of peas, Pisum sativum L. Z. Pflanzen Physiol. 100 : 79-83.
230. Mandahar, C.L. and I.D. Garg. 1975. Effect of ear removal on sugars and chlorophylls of barley leaves. Photosynthetica. 9 : 407-409.
231. Mansfield, T.A. and R.S. Jones. 1971. Effect of abscisic acid on potassium uptake and starch content of stomatal guard cells. Planta. 101 : 147-158.
232. Manyo, J.H. and W.J. Whittington. 1973. Genotypic differences in flag leaf area and their contribution to grain yield in wheat. Euphytica. 22 : 600-606.
233. Markham, R. 1955. Nucleic acids, their components and related compounds. In : Modern Methods of Plant Analysis, Vol. IV (eds. K. Paech and M.V. Tracey), pp. 246-304, Springer-Verlag, Berlin.
234. Martin, C. and K.V. Thimann. 1972. The role of protein synthesis in the senescence of leaves. I. The formation of protease. Plant Physiol. 49 : 64-71.

235. Martin, M. and B. Sabater. 1989. Translational control of chloroplast protein synthesis during the senescence of barley leaves. *Physiol. Plant.* 75 : 374-381.
236. Martin, M., Urteaga, B. and B. Sabater. 1986. Chloroplast protein synthesis during barley leaf growth and senescence, effect of leaf excision. *J. Exp. Bot.* 37 : 230-237.
237. Martin, P. 1982. Stem xylem as a possible pathway for mineral retranslocation from senescing leaves to the ear in wheat (Triticum aestivum Cultivar Kolibri). *Aust. J. Plant Physiol.* 9 : 197-207.
238. Martinoia, E., Dalling, M. J. and Ph. Matile. 1982. Catabolism of chlorophyll : demonstration of chloroplast localised peroxidative and oxidative activities. *Z. Pflanzenphysiol.* 107 : 269-279.
239. Marx, G. A. 1968. Influence of genotype and environment on senescence in peas. *Bioscience.* 18 : 505-506.
240. Matile, P. and F. Winkenbach. 1971. Function of Lysosomes and Lysosomal enzymes in senescing corolla of the morning glory (Ipomoea purpurea). *J. Exp. Bot.* 122 : 759-771.
241. Mattoo, A. K. and N. Aharoni. 1988. Ethylene and plant senescence. In : *Senescence and Ageing in Plants* (eds. L. D. Nooden and A. C. Leopold), pp. 241-280, Academic Press, New York.
242. Mauk, C. S. and L. D. Nooden. 1983. Cytokinin control of mineral nutrient distribution between the foliage and seeds in soybean explants. *Plant Physiol.* 72 (Suppl) : 167.
243. Mayak, S. and A. H. Halevy. 1980. Flower senescence. In : *Senescence in Plants* (ed. K. V. Thimann), pp. 131-156, CRC Press, Boca Raton, Florida.

244. McKersie, B.D., Senaratna, T., Walker, M.A., Kendall, E.J. and P.R. Hetherington. 1988. Deterioration of membranes during ageing in plants : Evidence for free radical mediation. In : Senescence and Ageing in Plants (eds. L.D. Nooden and A.C. Leopold), pp.441-464, Academic Press, New York.
245. Medawar, P.B. 1957. 'The Uniqueness of the Individual', ^{all in} Basic Book, New York. ^{original}
246. Miller, C.O. 1980. Cytokinin inhibition of respiration of mitochondria of six plant species. Proc. Natl. Acad. Sci. USA. 177 : 4731-4735.
247. Milthorpe, F.L. and J. Moorby. 1969. Vascular transport and its significance in plant growth. Ann. Rev. Plant Physiol. 20 : 117-138.
248. Mishra, S.D. and B.K. Gaur. 1972. Control of senescence in betel leaves by depetiolation. Exp. Gerontol. 7 : 31-35.
249. Mishra, S.D. and B.K. Gaur. 1986. Improving kernel weight through delay in flag leaf senescence of barley by plant growth regulators (PGRS). Ind. J. Exp. Biol. 24 : 328-329.
250. Mishra, D. and M. Kar. 1974. Nickel in plant growth and development. Bot. Rev. 40 : 395-452.
251. Misra, G. and U.C. Biswal. 1973. Factor concerned in leaf senescence. I. Effect of age, chemicals, petiole and photoperiod on senescence in detached leaves of Hibiscus rosa-sinensis L. Bot. Gaz. 134 : 5-11.
252. Mitra, R., Seal, S. and S.P. Sen. 1968. Nucleic acids and organ growth. In : Plant Growth Substances (ed. S.M. Sircar), Proc. Symp., Calcutta Univ., Calcutta, pp.113-120.

253. Molisch, H. 1938. The Longevity of plants. Translation of E.H. Fulling. Sci. Press, Lancaster.
254. Mondal, R. and M.A. Choudhuri. 1980. Another Rumex species responding to gibberellin bioassay by leaf senescence method. Sci. Cult. 46 : 361-362.
255. Mondal, R. and M.A. Choudhuri. 1981. Role of hydrogen peroxide in senescence of excised leaves of rice and maize. Biochem. Physiol. Pflanzen. 176 : 700-709.
256. Mondal, W.A. 1987. Studies in monocarpic senescence of some rice cultivars. Ph.D. Thesis, Burdwan University, Burdwan.
257. Mondal, W.A. and M.A. Choudhuri. 1984. Senescence behaviour of the whole plant in four rice cultivars. Experientia. 40 : 460-461.
258. Mondal, W.A. and M.A. Choudhuri. 1984. Sequential and non-sequential pattern of monocarpic senescence in two rice cultivars. Physiol. Plant. 61 : 287-292.
259. Mondal, W.A. and M.A. Choudhuri. 1985. Comparison of phosphorus mobilization during monocarpic senescence in rice cultivars with sequential and non-sequential leaf senescence. Physiol. Plant. 65 : 221-227.
260. Mondal, W.A., Dey, B.B. and M.A. Choudhuri. 1984. Proline accumulation as a reliable indicator of monocarpic senescence in rice cultivars. Experientia. 41:346-348.
261. Moorby, J. 1977. Integration and regulation of translocation within the whole plant. Symp. Soc. Exp. Biol. 31 : 425-454.
262. Moore, S. and W.W. Stein. 1948. Photometric ninhydrin method for use in the chromatography of amino acids. J. Biol. Chem. 176 : 367-388.
263. Mothes, K. 1960. Über des Altern der Blätter und die Möglichkeit ihrer Wiederverjüngung. Naturwissenschaften. 47 : 337-350.

264. Mothes, K. and L. Engelbrecht. 1952. Über geschlechtsverschieden Stoffwechsel zweihausiger einjähriger Pflanzen 1. Untersuchungen über den stickstoffumsatz beim Hanf (Cannabis sativa L.). Flora. 139 : 1-27.
265. Muller, K. and A.C. Leopold. 1966. Correlative ageing and transport of ³²P in corn leaves under the influence of kinetin. Planta. 68 : 167-185.
266. Murata, Y. and S. Matsushima. 1975. Rice In : Crop Physiology : Some Case Histories (ed. L.T. Evans), pp. 73-99, Cambridge Univ. Press, London.
267. Murayama, N. 1965. The influence of mineral nutrition on the characteristics of plant organs. In : The mineral nutrition of the rice plant. Proceedings of a Symposium at the International Rice Research Institute, February 1964. pp. 147-172, The Johns Hopkins Press, Baltimore, Maryland.
268. Murayama, N. and Y. Kawarasaki . 1957. Phosphorus nutrition of the soybean. I. Effect of period of phosphorus supply on growth and yield (Japanese). J. Sci. Soil. Manure. 28 : 191-193.
269. Murray, B.J., Mauk, C. and L.D. Nodden. 1982. Restricted vascular pipelines (and orthostichies) in plants. What's New in Plant Physiol. 13 : 33-35.
270. Murray, D.R. 1984. Seed Physiology, Vol. 2, Germination and Reverse Mobilization, Academic Press, Orlando, Florida.
271. Murumkar, C.V. and P.D. Chavan. 1988. Changes in photosynthetic carbon metabolism in senescent leaves of chick pea Cicer arietinum L. Acta Soc. Bot. Pol. 57 : 127-136.
272. Nath, N. and S.D. Mishra. 1990. Stimulation of ribulose-1,5-bisphosphate carboxylase activity in barley flag leaf by plant growth regulators. Photosynthetica. 24 : 266-269.

273. Neumann, P.M. 1987. Sequential leaf senescence and correlatively controlled increases in xylem flow resistance. *Plant Physiol.* 83 : 931-944.
274. Neumann, P.M. and L.D. Nooden. 1983. Interaction of mineral and cytokinin supply in control of leaf senescence and seed growth in soybean explants. *J. Plant Nutr.* 6 : 735-742.
275. Neumann, P.M. and L.D. Nooden. 1984. Pathway and regulation of phosphate translocation to the pods of soybean explants. *Physiol. Plant.* 60 : 166-170.
276. Neumann, P.M. and Z. Stein. 1983. Xylem transport and the regulation of leaf metabolism. *What's New in Plant Physiol.* 14 : 33-36.
277. Neumann, P.M. and Z. Stein. 1984. Relative rates of delivery of xylem solutes to shoot tissues : Possible relationship to sequential leaf senescence. *Physiol. Plant.* 62 : 390-397.
278. Neumann, P.M., Tucker, T. and L.D. Nooden. 1983. Characterization of leaf senescence and pod development in soybean explants. *Plant Physiol.* 72 : 182-185.
279. Nickel, B.E., Roth, S.Y., Cook, R.G., Allis, C.D. and J.R. Davie. 1987. Changes in histone H2A, variant H2A. Z and polyubiquitinated histone species in developing trout testis. *Biochemistry*, 26 : 4417-4421.
280. Nil, M., Kawano, S., Nakamura, S. and T. Kuroiwa. 1988. Changes in the fine structure of chloroplast and chloroplast DNA of peach leaves during senescence. *J. Japanese Soc. Hor. Sci.* 57 : 390-398.
281. Nooden, L.D. 1980. Senescence in the whole plant. In : *Senescence in Plants* (ed. K.V. Thimann), pp. 219-258, CRC Press, Boca Raton, Florida.
282. Nooden, L.D. 1980. Regulation of senescence. In : *Proceeding of World Soybean Research Conference* (ed. F.T. Corbin), pp. 139-152, Westview Press, Boulder, Colorado.

283. Nooden, L.D. 1984. Integration of soybean pod development and monocarpic senescence. *Physiol.Plant.* 62:273-284.
284. Nooden, L.D. 1985. Regulation of soybean senescence. In : *Proceeding of the World Soybean Research Conference. III.* (ed. R.Shibles), pp.891-900, Westview Press, Boulder, Colorado.
285. Nooden, L.D. 1986. Synergism between gibberellins and cytokinin in delaying leaf senescence in soybean explants. *Plant Cell,Physiol.* 27 : 577-579.
286. Nooden, L.D. 1987. Soybean seed growth. Regulatory mechanisms in the whole plant. In : *Models in Plant Physiology and Biochemistry* (eds. D.Newman and K.Wilson), Vol.2, pp.145-147, CRC Press, Boca Raton, Florida.
287. Nooden, L.D. 1988. The phenomena of senescence and ageing in plants. In : *Ageing and Senescence in Plants* (eds. L.D.Nooden and A.C.Leopold), pp.1-50, Academic Press, New York.
288. Nooden, L.D. 1988. Absciscic acid, auxin and other regulators of senescence. In : *Senescence and Ageing in Plants* (eds. L.D.Nooden and A.C.Leopold), pp.329-368, Academic Press, New York.
289. Nooden, L.D. 1988. Whole plant senescence. In : *Senescence and Ageing in Plants* (eds. L.D.Nooden and A.C.Leopold), pp.391-439. Academic Press, New York.
290. Nooden, L.D. and J.J.Guilamet. 1989. Regulation of assimilation and senescence by the fruit in monocarpic plants. *Physiol.Plant.* 77 : 267-274.
291. Nooden, L.D. and A.C.Leopold. 1978. Phytohormones and the endogenous regulation of senescence and abscission. In : *Phytohormones and related Compounds. A Comprehensive Treatise* (eds. D.S.Letham, P.B.Goodwin and T.J.V.Higgins), Vol.2, pp.329-369, Elsevier/North Holland, Biomedical Press, Amsterdam.

292. Nooden, L.D. and A.C. Leopold (eds.). 1988. Senescence and Ageing in Plants, Academic Press, New York.
293. Nooden, L.D. and D.S. Letham. 1984. Translocation of zeatin riboside and zeatin in soybean explants. J. Plant. Growth. Regul. 2 : 265-279.
294. Nooden, L.D. and C.S. Mauk. 1987. Changes in mineral composition of soybean xylem sap during monocarpic senescence and alterations by depodding, Physiol. Plant. 70 : 735-742.
295. Nooden, L.D. and B.J. Murray. 1982. Transmission of the monocarpic senescence signal via the xylem in soybean. Plant Physiol. 69 : 754-756.
296. Nooden, L.D. and W.R. Obermeyer. 1981. Changes in abscisic acid translocation during pod development and senescence in soybeans. Biochem. Physiol. Pflanzen. 176 : 859-868.
297. Nooden, L.D. and J.E. Thompson. 1985. Ageing and senescence in Plants. In : Handbook of the Biology and Ageing (eds. C.E. Finch and E.L. Schneider), 2nd Ed., pp. 105-127, Van Nostrand, Reinhold Co. New York.
298. Nooden, L.D., Kahanak, G.M. and Y. Okatan. 1979. Prevention of monocarpic senescence in soybeans with auxin and cytokinin. Science. 206 : 841-843.
299. Nooden, L.D., Rupp, D.C. and B.D. Derman. 1978. Separation of seed development from monocarpic senescence in soybeans. Nature (London). 271 : 354-357.
300. Nooden, L.D., Singh, S. and D.S. Letham. 1990. Correlation of xylem sap cytokinin levels with monocarpic senescence in soybean. Plant Physiol. 93 : 33-39.
301. Obata-Sasamoto, H. and H. Suzuki. 1979. Activities of enzymes related to starch synthesis and endogenous levels of growth regulators in potato stolon tips during tuberization. Physiol. Plant. 45 : 320-324.

302. Oritani, T. and R. Yoshida. 1973. Studies on nitrogen metabolism in crop plants. XII. Cytokinins and abscisic acid-like substances levels in rice and soybean leaves during their growth and senescence. *Proc. Crop. Sci. Japan.* 42 : 280-287.
303. Oritani, T. and R. Yoshida. 1976. Studies on nitrogen metabolism in crop plants. XIV. Changes in cytokinins in rice grains during ripening. *Proc. Crop. Sci. Soc. Japan.* 45 : 429-435.
304. Osborne, D.J. 1967. Hormonal regulation of leaf senescence. *Symp. Soc. Exp. Biol.* 21 : 179-213.
305. Osborne, D.J. 1980. Senescence in seeds. In : *Senescence in Plants* (ed. K.V. Thimann), pp.13-37, CRC Press, Florida.
306. Osborne, D.J. 1982. Deoxyribonucleic acid integrity and repair in seed germination : the importance in viability and survival. In : *The Physiology and Biochemistry of seed Development, Dormancy and Germination* (ed. A.A. Khan), pp.435-463, Elsevier, Amsterdam.
307. Osborne, D.J. 1985. Annual Plants. In : *Interdisciplinary Tropics in Gerontology*, Vol.21, (ed. H.P. Von Hann), pp.247-262, Karger, Basel.
308. Osborne, D.J. and K.S.E. Cheah. 1982. Hormones and foliar senescence. In : *Growth Regulators in Plant Senescence. Monogr. 8* (eds. M.B. Jackson, B. Grout and I.A. Mackenzie), pp.57-83, British Plant Growth Regulator Group. Wantage, Nottingham.
309. Osborne, D.J. and H.M. Hallaway. 1960. Auxin control of protein levels in detached autumn leaves. *Nature.* 188:240-241.
310. Osman, A.M. and F.L. Milthorpe. 1971. Photosynthesis of wheat leaves in relation to age, illuminance, and nutrient supply. II. Results. *Photosynthetica.* 5 : 61-70.

311. Ozuna,R., Yera,R., Ortega,K. and G.Tallman. 1985. Analysis of guard cell viability and action in senescing leaves of Nicotiana glauca (Graham), tree tobacco. *Physiol.Plant.* 79 : 7-10.
312. Palit,P., Kundu,A., Mondal,R.K. and S.M.Sircar. 1979. Source-sink control of dry matter production and photosynthesis in rice (Oryza sativa L.) plant after flowering. *Indian J.Plant Physiol.* 22 : 87-91.
313. Pallas,J.E. and S.J.Kays. 1982. Inhibition of photosynthesis by ethylene - a stomatal effect. *Plant Physiol.* 70 : 598-601.
314. Panse,V.G. and P.T.Sukhatme. 1976. Statistical methods for agricultural works (2nd edn.), pp.150-157, ICAR, New Delhi.
315. Park,J. and K.V.Thimann. 1990. Senescence and stomatal aperture as affected by antibiotics in darkness and light. *Plant Physiol.* 92 : 696-702.
316. Patel,K.R. 1980. Cytochemical studies on the relationship between DNA-histone ratio and endogenous RNA level in differentiating metaxylem cells. *Nucleus (Cal.)*. 23 : 67-69.
317. Patel,K.R. and G.P.Berlyn. 1982. Influence of kinetin on histone composition and endogenous RNA level in differentiating metaxylem of Zea mays root tips. *Caryologia.* 35 : 217-224.
318. Patterson,T.G. and W.A.Burn. 1980. Influence of sink removal in the senescence pattern of wheat. *Crop.Sci.* 20:19-23.
319. Pauls,K.P. and J.E.Thompson. 1984. Evidence for the accumulation of peroxidized lipids in membranes of senescing cotyledons. *Plant Physiol.* 75 : 1152-1157.
320. Peach,K. and U.F.Eberhardt. 1956. Altern und zelltod. In : *Hundbuch der pflanzen physiologie.* Bd. 25 : 908-936. Berlin-Gottingen, Heidelberg, Springer.

321. Peat, J.R. and B. Jeffcoat. 1982. The potential for increasing soybean yield with plant growth regulators. In : Chemical Manipulation of Crop Growth and Development (ed. J.S. McLaren), pp. 237-249, Butterworth, Scientific, London.
322. Peoples, M.B. and M.J. Dalling. 1978. Degradation of ribulose-1,5-bisphosphate carboxylase by proteolytic enzymes from crude extracts of wheat leaves. *Planta*. 138 : 153-160.
323. Peoples, M.B., Beilharz, V.C., Waters, S.P., Simpson, R.J. and M.J. Dalling. 1980. Nitrogen redistribution during grain growth in wheat (Triticum aestivum L). 21. Chloroplast senescence and the degradation of ribulose-1,5-bisphosphate carboxylase. *Planta*. 149 : 241-251.
324. Pesci, P. 1988. Ion fluxes and abscisic acid induced proline accumulation in barley leaf segments. *Plant Physiol.* 86 : 927-930.
325. Phillips, I.D.J. 1975. Apical dominance. *Annu. Rev. Plant Physiol.* 26 : 341-367.
326. Pillay, D.T.N. and J.H. Cherry. 1974. Changes in leucyl, seryl and tyrosyl t-RNAs in ageing soybean cotyledons. *Can. J. Bot.* 52: 2499-2504.
327. Pillay, D.T.N. and S. Gowda. 1981. Age related changes in transfer RNA species and transfer RNA synthesis in germinating soybean (Glycine max cultivar Harcor), cotyledons. *Gerontology*. 27 : 194-204.
328. Poovaiah, B.W. and A.C. Leopold. 1973. Deferral of leaf senescence with calcium. *Plant Physiol.* 52 : 236-239.
329. Proebsting, W.M., Davies, P.J. and G.A. Marx. 1978. Photoperiod-induced changes in gibberellin metabolism in relation to apical growth and senescence in genetic lines of peas (Pisum sativum L). *Planta*. 141 : 231-238.

330. Pryor, W.A. 1976. (ed) In : Free Radicals in Biology, Vol.1, pp.1-49, Academic Press, New York.
331. Purohit, S.S. 1982. Monocarpic senescence in Helianthus annuus. I. Relation of fruit induced senescence, chlorophyll and chlorophyllase activity. Photo-synthetica. 16 : 542-545.
332. Purohit, S.S. 1982. Prevention by kinetin of ethylene induced chlorophyllase activity in senescing detached leaves of Helianthus annuus. Biochem.Physiol.Pflanzen. 177 : 625-627.
333. Raghavendra, A.S. and K.B.Reddy. 1987. Action of proline on stomata differs from that of abscisic acid, G-substances or methyl jasmonate. Plant Physiol. 83 : 732-734.
334. Rajagopal, V. 1981. The influence of exogenous proline on the stomatal resistance in Vicia fava. Physiol.Plant. 52 : 292-296.
335. Rao, T.R.K. and M.C.Ghildiyal. 1985. Analysis of photo-synthetic source and sink relationship in mung bean Vigna radiata. Ind.J.Plant Physiol. 28 : 135-144.
336. Raschke, K. 1982. Involvement of abscisic acid in the regulation of gas exchange, evidence and inconsistencies In : Plant Growth Substances (ed. P.F.Wareing), pp.581-590, Academic Press, New York.
337. Raschke, K. and R.Hedrich. 1985. Simultaneous and independent effects of abscisic acid on stomata and the photosynthetic apparatus in whole leaves. Planta. 163 : 105-118.
338. Rawson, H.M., Gifford, R.M. and P.M.Bremner. 1976. Carbon dioxide exchange in relation to sink demand in wheat. Planta. 132 : 19-23.

339. Ray, S. and M.A.Choudhuri. 1981. Mobilization of metabolites from leaves to grains as the cause of monocarpic senescence in rice. *Plant Physiol.* 68 : 1345-1348.
340. Ray, S. and M.A.Choudhuri. 1982. Senescence mechanism in rice. *Proc.1st Conf.Assocn.Geront.(India)*, BHU (Varanasi), pp.89-93.
341. Ray, S. and M.A.Choudhuri. 1984. Senescence of rice leaves at the vegetative stage as affected by growth substances. *Biol.Plant.* 26 : 267-274.
342. Ray, S., Mondal, W.A. and M.A.Choudhuri. 1983. Regulation of leaf senescence, grain filling and yield of rice by kinetin and abscisic acid. *Physiol.Plant.* 59 : 343-346.
343. Reid, J.B. 1980. Apical senescence in Pisum : direct or indirect role for the flowering genes ? *Ann.Bot.* 45 : 195-201.
344. Rhodes, M.J.C. 1980. The maturation and ripening of fruits. In : *Senescence in Plant* (ed. K.V.Thimann), pp.157-205, CRC Press, Boca Raton, Florida.
345. Rhodes, M.J.C. 1980. Respiration and senescence of plant organs. In : *The Biochemistry of Plants. Metabolism and Respiration*, (ed. D.D.Davies), Vol.2, pp.419-462, Academic Press, New York.
346. Richmond, A.E. and A.Lang. 1957. Effect of kinetin on protein content and survival of detached Xanthium leaves. *Science.* 125 : 650-651.
347. Roberts, D.R., Thompson, J.E., Dumbroff, E.B., Gepstein, S. and A.K.Mattoo. 1987. Differential changes in the synthesis and steady-state levels of thylakoid proteins during bean leaf senescence, *Mol.Biol.* 9 : 343-353.

348. Romani, R.J. 1987. Mitochondrial activity during senescence
In : Plant Senescence : its Biochemistry and Physiology (eds. W.W. Thomson, E.A. Nothnagel and R.C. Huffaker),
pp. 81-88, Am. Soc. Plant. Physiol., Maryland.
349. Ross, J.R. and J.W. Bradbeer. 1971. Studies in seed dormancy.
V. The content of endogenous gibberellins in seeds of
Corylus avellana L. Planta. 100 : 288-302.
350. Roy Choudhuri, S. and M.A. Choudhuri. 1985. Hydrogen peroxide
metabolism as an index of water stress tolerance in
jute. Physiol. Plant. 65 : 503-507.
351. Sabater, B. 1984. Hormonal regulation of senescence. In :
Hormonal Regulation of Plant Growth and Development
(ed. S.S. Purohit), pp. 169-217, Agro Botanical Publication,
Bikaner, India.
352. Sabater, B. and M.T. Rodriguez. 1978. Control of chlorophyll
degradation in detached leaves of barley and oat
through effect of kinetin on chlorophyllase levels.
Physiol. Plant. 43 : 274-276.
353. Sabater, B., Rodriguez, M.T. and A. Zamorano. 1981. Effects
of interactions of gibberellic acid and cytokinins
on the retention of chlorophyll and phosphate in
barley leaf segments. Physiol. Plant. 51 : 361-364.
354. Sacher, J.A. and D.D. Davies. 1974. Demonstration of de novo
synthesis of RNase in Rhoeo leaf sections by deuterium
oxide labelling. Plant Cell Physiol. 15 : 157-162.
355. Sachs, J. 1982. Test Book of Botany (S.H. Vines, Transl.),
Clarendon Press, Oxford.
356. Saghir, A.R., Khan, A.R. and W. Worzella. 1968. Effects of
plant parts on grain yield, kernel weight and plant
height of wheat and barley. Agron. J. 60 : 95-97.

357. Saha, S., Nagar, P.K. and P.K. Sircar. 1986. Cytokinin concentration gradient in the developing grains and upper leaves of rice (Oryza sativa L) during grain-filling. Can.J.Bot. 64 : 2068-2072.
358. Salama, A.M.S., El-D.A. and P.F. Wareing. 1979. Effects of mineral nutrition on endogenous cytokinins in plants of sunflower (Helianthus annuus L). J.Exp.Bot. 30 : 971-981.
359. Salter, P.J. and D.H. Drew. 1965. Root growth as a factor in the response of Pisum sativum L. to irrigation. Nature. 206 : 1063-1064.
360. Samet, J.S. and T.R. Sinclair. 1980. Leaf senescence and abscisic acid in leaves of field grown soybean. Plant Physiol. 66 : 1164-1168.
361. Sandermann, H.Jr. 1978. Regulation of membrane enzymes by lipids. Biochem.Biophys.Acta, 515 : 209-237.
362. Saniewski, M., Czapski, J. and J. Nowacki. 1987. Relationship between stimulatory effect of methyl jasmonate or ethylene production and 1-aminocyclopropane-1-carboxylic acid content in tomatoes. Biol.Plant. 29 : 17-21.
363. Sankhla, N. 1971. Inhibition of abscisic acid induced chlorophyll degradation by potassium. Curr.Sci. 40 : 302-303.
364. Satler, S.O. and K.V. Thimann. 1983. Relation between respiration and senescence in oat leaves. Plant Physiol. 72 : 540-546.
365. Sattelmacher, B. and H. Marschner. 1978. Nitrogen nutrition and cytokinin activity in Solanum tuberosum. Physiol. Plant. 42 : 185-189.

366. Schwabe, W.W. and V.J.Kulkarni. 1987. Senescence-associated changes during long-day induced leaf senescence and the nature of the graft-transmissible senescence substances in Kleinia articulata. J.Exp.Bot. 38 : 1741-1755.
367. Scott, N.S. and J.V.Possingham. 1983. Changes in chloroplast DNA levels during growth of spinach leaves. J.Exp.Bot. 34 : 1756-1767.
368. Seal, S.N. and S.P.Sen. 1968. The role of growth substances in ageing tissue in relation to nucleic acid metabolism. In Plant Growth Substances (ed.S.M.Sircar), pp.171-185, Proc.Symp.Calcutta Univ., Calcutta.
369. Secor, J., Shibles, R. and C.R.Stewart, 1983. Metabolic changes in senescing soybean leaves of similar plant ontogeny. Crop.Sci. 23 : 106-110.
370. Seemann, J.R. and T.D.Sharkey. 1987. The effect of abscisic acid and other inhibitors on photosynthetic capacity and the biochemistry of CO₂ assimilation. Plant Physiol. 84 : 696-700.
371. Seidlova, F. and H.Sadlikava. 1983. Floral transition as a consequence of growth, changes in different components of the shoot apical meristem of Chenopodium rubrum. Biol.Plant. 25 : 50-62.
372. Sesay, A. and R.Shibles. 1980. Mineral depletion and leaf senescence in soybean (Glycine max) as influenced by foliar nutrient application during seed-filling. Ann.Bot. 45 : 47-55.
373. Setter, T.L., Burn, W.A. and M.L.Brenner, 1980. Stomatal closure and photosynthetic inhibition in soybean leaves induced by petiole girdling and pod removal. Plant Physiol. 65 : 884-887.

374. Setter, T.L., Burn, W.A. and M.L. Brenner. 1980. Effect of obstructed translocation on leaf abscisic acid and associated stomatal closure and photosynthesis decline. *Plant Physiol.* 65 : 1111-1115.
375. Setter, T.L., Burn, W.A. and M.L. Brenner. 1981. Abscisic acid translocation and metabolism in soybeans following depodding and petiole girdling treatments. *Plant Physiol.* 67 : 774-779.
376. Setterfield, G. and L. Fowke. 1957. Hormonal Regulation of Development of Cellular Organelles. Paper Presented at the Sixth International Conference on Plant Growth Substances. Ottawa, Canada.
377. Sexton, R. and H.W. Woolhouse. 1984. Senescence and abscission. In : *Advanced Plant Physiology* (ed. M.B. Wilkins), pp. 469-497, Pitman Publishing Ltd., London.
378. Sharkey, T.D. 1985. Photosynthesis in intact leaves of C_3 plants. Physics, physiology and rate limitation. *Bot. Rev.* 51 : 53-105.
379. Shimokawa, K. 1983. The role of ethylene in fruit ripening. In : *Aspects of Physiology and Biochemistry of Plant Hormones*. (ed. S.S. Purohit), pp. 275-300, Kalyani Publishers, New Delhi.
380. Shiner, T.L. 1979. The control of vascular development. *Annu. Rev. Plant Physiol.* 30 : 313-337.
381. Shyr, Y.Y. and C.H. Kao. 1985. Senescence of rice leaves. XV. Solute leakage and inorganic phosphate uptake. *Bot. Bull. Acad. Sin.* 26 : 171-178.
382. Simon, E.W. 1967. Types of leaf senescence. *Soc. Exp. Biol. Symp.* 21 : 215-225.
383. Sinclair, T.R. and C.T. de Wit. 1975. Photosynthate and nitrogen requirements for seed production by various crops. *Science*. 189 : 565-567.

384. Sitton,D., Itai,C. and H.Kende. 1967. Decreased cytokinin production in the roots as a factor in shoot senescence. *Planta*. 73 : 296-300.
385. Sjut,V. and F.Bangerth. 1984. Induced perthenocarp - a way of manipulating levels of endogenous hormones in tomato fruit (*Lycopersicon esculentum* Mill). *Z.Diffusible Hormones. Plant Growth Regul.* 2 : 49-56.
386. Smith,O.E., Lyon,J.L., Addicott,F.T. and R.E.Johnson. 1968. Abscission physiology of abscisic acid. In : *Physiology of Plant Growth Substances*. (eds. F.Wrightman and G.Setterfield), pp.1547-1560, Runge Press, Ottawa.
387. Snell,F.D. and C.T.Snell. 1971. *Colorimetric Method of Analysis*, Vol.II, AAA, Van Nostrand, Reinhold Co., New York, pp.26-27.
388. Spiker,S. 1988. Histone variants and high mobility group non-histone chromosomal proteins of higher plants : Their potential for forming a chromatin structure that is either poised for transcription or transcriptionally inert. *Physiol.Plant.*75 : 200-213.
389. Srivastava,B.I.S. 1968. Acceleration of senescence and of the increase in chromatin-associated nucleases in excised barley leaves by abscisin-II and its reversal by kinetin. *Biochem.Biophysics.Acta*. 169 : 535-536.
390. Stedman,E. and E.Stedman. 1950. Cell Specificity of histones. *Nature*. 166 : 280-281.
391. Stephenson,A.G. 1981. Flower and fruit abortion : proximate causes and ultimate functions. *Ann.Rev.Ecol.Syst.* 12 : 253-279.
392. Stewart,C.R. 1980. The mechanism of abscisic acid induced proline accumulation in barley leaves. *Plant Physiol.* 66 : 230-233.

393. Stewart, C.R. 1981. Proline accumulation : biochemical aspects. In : *The Physiology and Biochemistry of Drought Resistance in Plants* (eds. L.G.Paleg and D.Aspinall), Academic Press, USA.
394. Stewart, C.R. and G.Voetberg. 1985. Relationship between stress-induced ABA and proline accumulation and ABA induced proline accumulation in excised barley leaves. *Plant Physiol.* 79 : 24-27.
395. Stewart, C.R., Voetberg, G. and P.J.Rayapati. 1986. The effects of benzyladenine, cycloheximide and cordycepin on wilting-induced abscisic acid and proline accumulations and abscisic acid and salt induced proline accumulation in barley leaves. *Plant Physiol.* 82 : 703-707.
396. Storey, R. and L.Beevers. 1977. Proteolytic activity in relation to senescence and cotyledonary development in Pisum sativum L. *Planta.* 124 : 77-87.
397. Suzuki, S., Nakamoto, H., Ku, M.S.B. and G.E.Edwards. 1987. Influence of leaf age on photosynthesis, enzyme activity and metabolite levels in wheat. *Plant Physiol.* 84 : 1244-1248.
398. Takegami, T. 1975. A study on senescence in tobacco leaf discs. II. Chloroplast and cytoplasmic r-RNAs. *Plant Cell Physiol.* 16 : 417-425.
399. Tamas, I.A., Engels, C.J., Kaplan, S.L., Ozbun, J.L. and D.H.Wallace. 1981. Role of indoleacetic acid and abscisic acid in the correlative control by fruits of axillary bud development and leaf senescence. *Plant Physiol.* 68 : 476-481.
400. Tappel, A.L. 1980. Measurement of and protection from in vivo lipid peroxidation. In : *Free Radicals in Biology* (ed. W.A.Pryor), Vol.IV, pp.1-47, Academic Press, USA.

401. Tetley, R.M. and K.V. Thimann. 1974. The metabolism of oat leaves during senescence. I. Respiration, carbohydrate metabolism and the action of cytokinins. *Plant Physiol.* 54 : 294-303.
402. Thayer, S.S. and R.C. Huffaker. 1984. Vacuolar localisation of endoproteinases EP₁ and EP₂ in barley mesophyll cells. *Plant Physiol.* 75 : 70-73.
403. Thimann, K.V. 1980. The senescence of leaves. In : *Senescence in Plants* (ed. K.V. Thimann), pp. 86-115, CRC Press, Boca Raton, Florida.
404. Thimann, K.V. 1985. The senescence of detached leaves of Tropaeolum. *Plant Physiol.* 79 : 1107-1110.
405. Thimann, K.V. 1987. Plant Senescence : A proposed integration of the constituent processes. In : *Plant Senescence : its Biochemistry and Physiology* (ed. W.W. Thomson, E.A. Nothnagel and R.C. Huffaker), pp. 1-19, Am. Soc. Plant. Physiol. Maryland.
406. Thimann, K.V. 1988. Foreword In : *Senescence and Ageing in Plants* (eds. L.D. Nooden and A.C. Leopold), pp. XVII-XXV, Academic Press, New York.
407. Thimann, K.V. and S.O. Satler. 1979. Relation between senescence and stomatal opening : Senescence in darkness. *Proc. Natl. Acad. Sci. USA.* 76 : 2770-2773.
408. Thomas, H. 1977. Ultrastructure polypeptide composition and photochemical activity of chloroplasts during foliar senescence of a nonyellowing mutant genotype of Festuca pratensis Huds. *Planta.* 137 : 53-60.
409. Thomas, H. and P. Hilditch. 1987. Metabolism of thylakoid membrane proteins during foliar senescence. In : *Plant Senescence : its Biochemistry and Physiology* (ed. W.W. Thomson, E.A. Nothnagel and R.C. Huffaker), pp. 114-122. The Am. Soc. Plant Physiol. Maryland.

410. Thomas, H. and J.L. Stoddart. 1980. Leaf senescence. *Annu. Rev. Plant Physiol.* 31 : 83-111.
411. Thompson, J.E. 1988. The molecular basis for membrane deterioration during senescence. In : *Senescence and Ageing in Plants* (eds. L.D. Nooden and A.C. Leopold), pp. 51-83, Academic Press, New York.
412. Thompson, J.E., Mayak, S., Shinitzky, M. and A.H. Halevy. 1982. Acceleration of membrane senescence in cut carnation flowers by treatment with ethylene. *Plant Physiol.* 69 : 859-863.
413. Thompson, J.E., Paliyath, G., Brown, J.H. and C.L. Duxbury. 1987. The involvement of activated oxygen in membrane deterioration during senescence. In : *Plant Senescence : its Biochemistry and Physiology* (eds. W.W. Thomson, E.A. Nothnagel and R.C. Huffaker), pp. 146-155, Am. Soc. Plant Physiol. Maryland.
414. Thorne, G.N. 1965. Photosynthesis of ears and flag leaves of wheat and barley. *Ann. Bot.* 32 : 79-82.
415. Thorne, G.N., Ford, M.A. and D.J. Watson. 1968. Growth, development and yield of spring wheat in artificial climate, *Ann. Bot.* 32 : 425-446.
416. Thorne, J.H. and H.R. Koller. 1974. Influence of assimilate demand on photosynthesis, diffusive resistances, translocation and carbohydrate levels of soybean leaves. *Plant Physiol.* 54 : 201-207.
417. Tosh, S., Choudhuri, M.A. and S.K. Chatterjee. 1979. Retardation of lettuce (*Lactuca sativa* L.) leaf senescence by cobalt ions. *Ind. J. Exp. Biol.* 17 : 1134-1136.
418. Trewavas, A.J. 1982. Growth substance sensitivity : The Limiting factor in plant development. *Physiol. Plant.* 55 : 60-72.

419. Turgeon, R., and J.A. Webb. 1975. Physiological and structural ontogeny of the source leaf. In : Phloem Transport (eds. S. Arnoff, J. Dainty, P.R. Gorham, L.M. Srivastava and C.A. Swanson), pp.297-313, Plenum Press, New York.
420. Udovenko, G.V. and L.A. Gogoleva. 1974. Dynamics of DNA and RNA content in leaves of wheat during ontogenesis. Fiziol. Rast. (Moscow), 21 : 1076-1078.
421. Valio, I.F.M. and J.M. Polo. 1983. Reproductive structures on senescence of bean plants. Revta. Brasil. Bot. 6 : 99-102.
422. Van Staden, J. and J.E. Davey. 1979. The synthesis, transport and metabolism of endogenous cytokinins. Plant Cell Physiol. 2 : 93-106.
423. Van Staden, J., Cook, E.L. and L.D. Nooden. 1988. Cytokinins and senescence. In : Senescence and Ageing in Plants (eds. L.D. Nooden and A.C. Leopold), pp.281-328, Academic Press, New York.
424. Veierskov, B. and K.V. Thimann. 1988. The control of protein breakdown and synthesis in the senescence of oat leaves. Physiol. Plant. 72 : 257-264.
425. Veillon, J.M. 1971. Une Apocynaceae monocarpique de Nouvelle-Caledonie Cerberiopsis candelabrum Vieill. Adansonia. 11 : 625-639.
426. Villiers, T.A. 1980. Ultrastructural changes in seed dormancy and senescence. In : Senescence in Plants (ed. K.V. Thimann), pp.39-66, CRC Press, Florida.
427. Vogel, A.I. 1959. A Text Book of Practical Organic Chemistry Including Quantitative Organic Analysis, (3rd Ed.), Longmans Publ., New York, pp.969-973.
428. Vogel, A.I. 1961. A Text Book of Quantative Inorganic Analysis. The English Language Book Soc. and Longman Green and Co.Ltd., London, pp.783-784.

429. Walton, D.C. 1980. Biochemistry and Physiology of abscisic acid. *Annu. Rev. Plant Physiol.* 31 : 453-489.
430. Wang, C.Y., Cheng, S.H. and C.H. Kao. 1982. Senescence of rice leaves. VII. Proline accumulation in senescing excised leaves. *Plant Physiol.* 69 : 1348-1349.
431. Wang, T.L. and H.W. Woolhouse. 1982. Hormonal aspects of senescence in plant development. In : *Growth Regulators in Plant Senescence* (eds. M.B. Jackson, B. Grout and I.A. Mackenzie), Monogr. No. 8, pp. 5-25. Br. Plant Growth Regul. Group. Wantage, Nottingham.
432. Wangermann, E. 1965. Longevity and ageing in plants and plant organs. In : *Handbuch der Pflanzenphysiologie*. Vol. 15/2 (ed. W. Ruhland), pp. 1026-1057, Springer-Verlag, Berlin.
433. Wansch, A.M. and J. Lough. 1987. Modulation of histone H3 variant synthesis during the myoblast-myotube transition of chicken myogenesis. *Dev. Biol.* 119 : 94-99.
434. Wardley, T.M., Bhalla, P.L. and M.J. Dalling. 1984. Changes in the number and composition of chloroplasts during senescence of mesophyll cells of attached and detached primary leaves of wheat (Triticum aestivum L). *Plant Physiol.* 75 : 421-424.
435. Wareing, P.F. 1977. Growth substances and integration in the whole plant. *Symp. Soc. Exp. Biol.* 31 : 337-365.
436. Wareing, P.F. and A.K. Seth. 1967. Ageing and Senescence in the Whole Plant. *Symp. Soc. Exp. Biol.* 21 : 543-558.
437. Watanabe, A. and H. Imaseki. 1982. Changes in translatable m-RNA in senescing wheat leaves. *Plant Cell Physiol.* 23 : 489-490.
438. Waters, S.P., Peoples, M.B., Simpson, R.J. and M.J. Dalling. 1980. Nitrogen redistribution during grain growth in wheat (Triticum aestivum L.). I. Peptide hydrolase activity and protein breakdown in the flag leaf, glumes and stem. *Planta.* 146 : 422-428.

439. Waters, S.P., Noble, E.R. and M.J. Dalling. 1982. Intracellular localization of peptide hydrolases in wheat (Triticum aestivum L.). Plant Physiol. 69 : 575-579.
440. Weber, F. 1919. Der naturliche Tod der Pflanzen. Naturwiss. Wochenschr. 18 : 447-457.
441. Williams, P.W., and M. Sicardi de Mallorca. 1982. Absciscic acid and gibberellin-like substances in roots and root nodules of Glycine max. Plant Soil. 65 : 19-26.
442. Wittenbach, V.A. 1979. Ribulose biphosphate carboxylase and proteolytic activity in wheat leaves from anthesis through senescence. Plant Physiol. 64 : 884-887.
443. Wittenbach, V.A. 1982. The effect of pod removal on leaf senescence in soybeans. Plant Physiol. 70 : 1544-1548.
444. Wittenbach, V.A. 1983. Effect of pod removal on leaf photosynthesis and soluble protein composition of field grown soybeans. Plant Physiol. 73 : 121-124.
445. Wittenbach, V.A., Ackerson, R.C., Giaquinta, R.T. and R.R. Hebert. 1980. Changes in photosynthesis, ribulose biphosphate carboxylase, proteolytic activity and ultrastructure of soybean leaves during senescence. Crop.Sci. 20:225-231.
446. Wood, L.J., Murray, B.J., Okatan, Y. and L.D. Nooden. 1986. Effect of petiole phloem disruption on starch and mineral distribution in senescing soybean leaves. Am.J.Bot. 73 : 1377-1383.
447. Woodrow, L., Jiao, J., Tsujita, M.J. and B. Grodzinski. 1989. Whole plant and leaf steady state gas exchange during ethylene exposure in Xanthium strumarium L. Plant Physiol. 90 : 85-90.
448. Woodson, W.R. 1987. Changes in protein and m-RNA populations during the senescence of carnation petal. Physiol.Plant. 71 : 495-502.

449. Woolhouse, H.W. 1967. The nature of senescence of plants.
In : Aspects of the Biology of Ageing (ed. H.W. Woolhouse), pp.179-213, Symp.Soc.Exp.Biol. Cambridge Univ. Press, London.
450. Woolhouse, H.W. 1974. Longevity and Senescence in Plants.
Sci.Prog. 61 : 123-147.
451. Woolhouse, H.W. 1981. Hormonal control of senescence allied to reproduction in plants. In : Strategies of Plant Reproduction, Beltsville Symposia in Agricultural Research. VI. (ed. W.J.Meudt), pp.201-233. US Dept. Agric., Beltsville, Allanheld, Osmun, Totowa.
452. Woolhouse, H.W. 1982. Leaf senescence. In : The Molecular Biology of Plant Development (eds. H.Smith and D.Grierrson), pp.256-281, Blackwell, Oxford.
453. Woolhouse, H.W. 1983. The general biology of plant senescence and the role of nucleic acid and protein turnover in the control of senescence process which are genetically programmed. In : Post-harvest Physiology and Crop Preservation (ed. H.Lieberman), pp.1-43, Plenum Press, New York.
454. Woolhouse, H.W. 1984. The biochemistry and regulation of senescence in chloroplasts. Can.J.Bot. 62 : 2934-2942.
455. Woolhouse, H.W. 1987. Regulation of senescence in the chloroplast. In : Plant senescence : its Biochemistry and Physiology (eds. W.W.Thomson, E.A.Nothing and R.C. Huffaker), pp.132-145, Am.Soc.Plant Physiol. Maryland.
456. Woolhouse, H.W. and G.I.Jenkins. 1983. Physiological responses, metabolic changes and regulation during leaf senescence, In : The Growth and Functioning of Leaves (eds. J.E.Dale and F.L.Milthorpe), pp.449-487, Cambridge Univ. Press, Cambridge.

457. Wright, S.T.C. 1975. Seasonal changes in the levels of free and bound abscisic acid in black currant (Ribes nigrum) buds and beech (Fagus sylvatica) buds. J.Exp.Bot. 26 : 161-174.
458. Yang, S.F. and N.E.Hoffman. 1984. Ethylene biosynthesis and its regulation in higher plants. Annu.Rev.Plant Physiol. 35 : 155-189.
459. Yu, S.M. and C.H.Kao. 1981. A comparison of activities of various cytokinins on the senescence of soybean Glycine max L. leaf discs. Bot.Bull.Acad.Sin. 22 : 49-56.
460. Yu, S.M. and C.H.Kao. 1983. Effect of benzyladenine on protein metabolism in soybean leaf discs during senescence. Bot.Bull.Acad.Sin. 24 : 65-70.
461. Zeiger, E. and A.Schwartz. 1982. Longevity of guard cell chloroplasts in falling leaves : Implication for stomatal function and cellular ageing. Science. 218 : 680-682.
462. Zimmerman, M.H. 1983. Xylem Structure and the Ascent of Sap, pp.66-82, Springer-Verlag, Berlin.

LIST OF PUBLISHED AND ACCEPTED PAPERS

1. Khan,R.I. and M.A.Choudhuri. 1988. Implication of changes in RNA and histone content during monocarpic senescence of wheat. Indian J.Exp.Biol. 26 : 621-624.
2. Khan,R.I. and M.A.Choudhuri. 1988. Changes in enzyme activities related to hydrogen peroxide metabolism during senescence of wheat plant. Indian J.Plant. Physiol. 31 : 97-101.
3. Khan,R.I. and M.A.Choudhuri. 1988. Changes in protein, nucleic acid and histone content in the shoot apex during panicle initiation and in the leaves during monocarpic senescence in rice plant. Science and Culture. 54 : 369-371.
4. Khan,R.I. and M.A.Choudhuri. 1991. Senescence behaviour of some rice cultivars. Indian J.Exp.Biol. 29 : 59-61.
5. Khan,R.I. and M.A.Choudhuri. 1991. Effect of spikelet removal on the whole plant senescence of rice. Biol.Plant - (in press).